This book is a collection of papers by N. Bernstein which
have been translated into English from Russian and
German.

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FOREWORD TO THE ENGLISH EDITION

UNFORTUNATELY the Author died on 16 January 1966, a few months prior to his seventieth birthday and before the publication of his work into English.

Professor Nicholas Bernstein was one of the great Russian physiologists who started a special branch of Physiological Science—the *physiology of activity*.

A man with a brilliant mind, an outstanding physiologist and mathematician, equally gifted in Science and in Art, he started his work in the twenties with a series of studies on the physiology of human motion. Using the cyclographic method and mathematical analysis of human movement, he formulated some general laws of the organization of human movements. In 1926 he published his well-known work on *General Biomechanics*, and in 1935, twelve years before the famous publication of Norbert Wiener, he formulated some basic principles of self-regulatory systems and the role of feedback in the regulation of man's voluntary movement. Twelve years later he completed his basic book, *The Construction of Movements*, which was published in Russian (1947). Here he described the basic levels of the organization of movements, starting with the elementary—spinal and subcortical levels—and ending with a sophisticated description of different cortical levels—the "spatial", "object" and "symbolic" ones. Here he formulated the basic rules of self-regulating movements of the man; he mentioned that it is impossible to control the plastic and changing movements by efferent impulses only, and formulated the role of the afferent feedback for the control of human actions. The description of the basic rules of the self-regulating systems underlying the movement of man, formulated in this book, was a result of the sophisticated physiological and mathematical work of Professor Bernstein, the leading authority in this chapter of human physiology.

In the latter part of his life—the fifties and sixties—Professor Bernstein was engaged in the generous task of including his findings in a rather philosophical system of "Physiology of Activity" cybernetical in its structure and biological in its context. The ideas of the rela-

tion of the models of Future *(Soll-Wert)* to their real ...tion in the Present activities *(Ist-Wert)*, the basic principles of probabilistic approach to the organization of the goal-directed behaviour, the ideas of a new deterministic solution of the old problem of activity—all these ideas have found a new shape, and are equally important both for biology and psychology, as well as for mathematics and philosophy.

The reader will find in this book the brilliant essays of a great man of science and, no doubt, the ideas contained in these essays will have a marked influence on the future work in these fields.

The late Professor Bernstein was a man who had the remarkable gift of penetrating into the future, and generations of biologists, physiologists and psychologists will be grateful to him for his generous endeavour.

Moscow

March 1966   A. R. LURIA

PREFACE

THE aim of this small collection of papers is to acquaint the reader with some fundamental conclusions gained from nearly 40 years of experimental and theoretical research into the control and regulation of human motor functions. The work has been carried out by my colleagues and myself by means of the cyclogrametric methods worked out in our laboratories. We have studied systematically and with the highest possible accuracy a great variety of movements in children, adults and old people, in both normal and clinical conditions, as well as in everyday life, work and sport. The articles published here cannot, of course, cover the complete range of our experimental findings, or even all of the most reliable and significant ones.

This collection has another important purpose, however. I have set out to show the general physiological conclusions that can be drawn, and the important changes in theory that can result, from the thorough and minutely detailed study of the co-ordination and regulation of motor functions. Such an analysis of the most important aspects of the vital activity of higher organisms has not yet been accorded the place in physiology which it deserves, but as it develops it promises to be of the greatest value in cybernetics and in the exact mathematical formulation of a physiological theory of motor behaviour.

Moscow   N. BERNSTEIN

PREFACE TO THE ENGLISH EDITION

THIS small collection includes papers which, although published at various times over a period of many years, form a coherent whole. The object of these studies is to illuminate the main problems and topics which have arisen in the course of 40 years of experimental and theoretical analyses of the regulation and control of human motor acts. The investigations were undertaken by means of the cyclogramatic method developed by our Unit, and described during this period in a series of publications [see Refs. 8, 12, 16, 18, 21 and 26]. This technique has been shown to be an extremely valuable tool for the detailed investigation of the structure and co-ordination of motor acts. The author and his colleagues* have used this technique in a large number of studies (which are far from completely represented in the bibliography), examining a whole series of movements encountered in industrial, athletic and artistic activities† and a wide range of locomotor activities of various types.‡

The papers incorporated in this text naturally cannot, and do not, purport to describe our experimental results in their entirety, or even to deal adequately with our most detailed and significant studies. This collection has another object. The author has tried to show how problems of general physiology can be explored in terms of the structural analysis of movements, how they may be set against a wide range of evidence from general physiology, dynamical anatomy and clinical studies and how, often, very significant changes and shifts in point of view on the regulation of motor acts arise from the necessity to study these acts in the most microscopic detail, and with the widest possible synthetic grasp of experimental

* L. Chkhaïdze, D. Donskoi, V. Gurfinkel, S. Kossilov, L. Ossipov, T. Popova, N. Sadchikov, O. Salzgeber, P. Spielberg *et al.*

† Cutting with a chisel, punching, stamping, striking keys in piano-playing, kicking in football, skiing, cycling, etc.

‡ Normal free walking, carrying weights, the changes of pace with fatigue, the development of walking in childhood and its involution in old age, various styles of running in sport, marching, the interruption and the redevelopment of walking after amputation and as a result of damage to the central nervous system, etc.

evidence. The science of human movements and theories of motor co-ordination have until recently been one of the most obscure branches of human and comparative physiology; the author has allowed himself to hope that the present text may, if only in small measure, contribute some momentum to an increasing interest in problems of the programming and control of voluntary motor acts, among psychologists, and, in particular, among cyberneticists.

The author wishes also to use this preface to express his sincere gratitude to the editorial staff of Pergamon Press and to Professor R. J. Drillis, Senior Research Scientist of New York University, for the great care and insight with which they have carried out their difficult task.

Moscow

N. BERNSTEIN

CHAPTER I

THE TECHNIQUES OF THE STUDY OF MOVEMENTS

(Published in *Textbook of the Physiology of Work*, edited by G. Conradi, V. Farfel and A. Slonim, Moscow, 1934)

1. The Cinematographic Study of Movements

Human movements have long been of great interest to investigators. Attempts have been made to observe and measure them for a considerable time. In the beginning of the 19th century the brothers Weber [76] carried out an extensive study of walking, employing the primitive observational techniques of their period—measuring lines and diopters. However, the rapid sequential patterns of human movements would have made precise observation unattainable if special opportunities had not arisen; these opportunities could be realized by the experimenter only with the development of instantaneous photography in the sixties of the 19th century. It was at just this time that energetic attempts to decipher the physiological mechanisms of human motor skills were begun; the end of the 19th century is marked in our field by such outstanding studies as those of Muybridge in the United States, Marey in France, and Braune and Fischer in Germany. The methodological innovations of the first two authors form the basis of later developments in cinematography; the last two authors laid the foundations of rigorously scientific quantitative investigation of movements with the help of photography.

It is not necessary in our own time to prove the value of cinematography as a technique for the study of movements; it provides an opportunity to record and to fix the rapidly interchanging phases of live movements in order to subsequently analyse them with any required degree of accuracy. Figure 1 presents a series of successive phases of fast running by a human being, taken by synchronizing

two cameras from separate view points. These photographs were taken by Muybridge in 1887 and are evidence of the high technical level attained by this forefather of cinematography.

It can be seen in Fig. 1 that the right leg later assumes the position which was earlier occupied by the left leg in the sixth frame; there is a correspondence, for example, between frames 1 and 7, 2 and 8, and so on. In this way a single step is spread out over 6 frames. This corresponds, in the given series, to a frequency of 24 frames per sec; during this period of time the subject could accomplish 4 single steps. For comparison we may observe that in contemporary cinematography the standard frequencies are 16 frames per sec for silent films, and 24 frames per sec for films with a sound track. At the present time high-speed cameras have shutter speeds of 160, 400 and even 1500 frames per sec. A single step of Muybridge's run would be broken down by these later cameras (Zeiss system) into 375 separate frames.

It may easily be imagined what occurs if motion-picture films exposed in high-speed processes are projected through conventional cinematographic equipment. Four hundred frames taken by a high-speed camera in 1 sec may be run through a projector which operates at 16 frames per sec over the period 400/16 = 25 sec; consequently, we may examine on the screen events photographed in the course of a single second. The time is increased, as it were, by a factor of 25; the term "time magnification" which has been applied to high-speed cameras can be justified in this way. Events which take place quickly in nature can be made many times slower, permitting leisurely examination of all their temporal details. Bernstein and Dement'ev [17] have constructed a special motion-picture projector allowing smooth projection on a screen at a frequency of 4–5 images per sec, that is, one-third or one-fourth as fast as the normal projection rate. This technique allows an increase in the augmentational effect of time magnification and it is possible, for example, to examine the high-speed camera photographs referred to above with a time augmentation of 400/4 = 100 times.

2. Cyclography—the Planar Projection of Movements

Marey introduced another method which, after numerous improvements of his basic idea, has come to occupy an unconditionally

predominant place in the study of movement. Separate, independent cinematographic exposures illustrate every phase of a movement excellently but they do not give a direct representation of the inter-relations between successive phases. In the photographs in Fig. 1 there are positions but not movements. It cannot be seen from them in what direction or with what velocity any given joint of the body is moving at the moment when a single exposure is made. These elements of a movement, its direction and velocity, are clearly visible by projection of the film on a screen but they can still only be observed by the naked eye and not by means of measuring instruments. Cine-film reproduces the movement in its entirety, but fixes in a form convenient for scientific measurement merely positions and isolated phases. Marey's idea consisted in recording on the photograph all the dynamic changes in the phases of the movement.

In order to achieve this, Marey isolated from the rest of the subject's body narrow strips on the long axes of the limbs and made them luminous while keeping the rest of the subject's body black so as not to record on the photographic emulsion (Fig. 2). He then photographed the subject, in this clothing, many times on a single plate in the course of making a movement (Fig. 3). As a result multiple images were obtained—chronophotography—providing a perfect opportunity to measure the directions and velocities of movements of particular points of the body. Braune and Fischer improved this technique by replacing Marey's tapes with Geisler tubes which provided intermittent light at intervals of 26 per sec. A photograph of walking taken by Braune and Fischer is given in Fig. 4.

Marey's school (Bulle, Gastine) replaced the tapes by points; in order to do this they fixed miniature incandescent bulbs to the points of the body under investigation. This alteration in technique, as adopted by American (Gilbreth, Townsend) and German (Thun) investigators, was termed cyclography. The Moscow School of Biometrics developed the cyclographic technique to a high degree in comparison with the forms in which it was employed in the West; for this reason the most useful approach will be to describe the current status of cyclography in terms of the studies carried out by this school. A typical cyclogram of walking is given in Fig. 5.

Small electric bulbs (Fig. 6) are fixed at the points of the subject's body that are to be photographed. If necessary, flashlight

bulbs may be used for the light (Fig. 6(c)), but tiny gas-filled bulbs (Fig. 6(b)) with a spiral filament, as prepared by F. Wolf in Berlin for Bernstein's project, are more suitable and provide ideal point representations because their filaments are only 1 mm in length. The bulbs are most frequently fixed over the centres of joints. The current (at a potential of 3–5 V) is led to the bulbs through thin flex from a belt worn by the subject; it is led to the latter through thin six-strand flex—a "tail"—20–80 m long, and thus not interfering with any movements, even running, which is connected to the experimenter's distribution board. It is also possible to supply the bulbs from dry batteries worn by the subject, but then they cannot be controlled from a distance, and it is often very important.

A cyclogram of uncomplicated movements (e.g. walking or running) is recorded on a fixed plate placed in a standard camera. If the subject carries out a movement in front of the camera with bulbs lit when the lens is uncovered, the displacement of each bulb will be represented on the photograph by a single continuous curve. In order to break down the image of the movement into distinct successive phases—to obtain a chronogram—the exposure is made through a rapidly rotating shutter (an interrupter, Fig. 7) which covers the lens for very brief periods at equal intervals some tens or hundred times a second. When the lens shutter is open the light from all the bulbs falls simultaneously on the plate and then is immediately blocked out when the lens is again covered. For this reason all the dots (Fig. 5) into which the rotating shutter breaks the different traces of the bulb trajectories correspond closely to each other in time. If points from adjacent trajectories which correspond to each other in time are joined by straight lines, schemata of successive positions of the movement are obtained which are exactly similar to the chronophotographs of Marey and Fischer (Fig. 8; see also Fig. 27(a)). With the help of a rotating shutter it is easy to obtain frequencies of up to 600 per sec, i.e. higher than are given by Debri's high-speed camera; it is difficult to operate faster than this frequency as the points of the trajectory then begin to merge into each other. We will not touch here on auxiliary techniques employed for more reliable identification of corresponding points of merging trajectories.

Exact measurement of the frequencies given by the rotating shutter is essential for the quantitative study of movements. A siren device employed by the Moscow school is very useful in this

respect, the technique being based on determination of the frequency of a tone emitted by a siren located on the shutter and rotating with it. This device, with a series of auxiliary devices, permits accuracy within a fraction of one per cent in the determination of frequencies. Mukhin's technique, employing the characteristics of neon bulbs, is even more accurate. Bernstein's measuring device, called a strobometer, is constructed on this principle and consists of an accurately calibrated electromagnetic tuning-fork, a low frequency amplifier and a neon bulb. Oscillations of the tuning-fork are amplified and control the neon bulb which goes on and off in synchrony with the oscillations. The bulb illuminates a small circle of concentric asterisks fixed on the axis of the rotating shutter. If the rotation speed is regulated with a rheostat so that the asterisk intermittently illuminated by the neon bulb appears to be motionless, the speed will be exactly syncronous with the oscillations of the tuning-fork. It is possible to calibrate it within some thousandths of one per cent with this apparatus. The advantage of Mukhin's method over the siren lies in the fact that several rotating shutters may be very accurately synchronized so as to work together, that it to say, the movement may be studied from different angles with several cameras. The action of the shutter may be rendered even more accurate if a frequency stabilizer with a Lacour wheel is coupled to the drive motor. The low frequency source for these stabilizers may be obtained from a sound-frequency oscillatory circuit with a subsequent stage of amplification.

Cyclography, in the form just described, is a poor device for the investigation of cyclical overlapping movements—to which category the majority of industrial processes belong: in movements of this type the images of the trajectories of the bulbs on a stationary plate appear as overlapping undifferentiable tangles. In order to overcome this inadequacy in cyclography Bernstein introduced kymocyclography [12], i.e. cyclographical exposures on slowly and evenly moving photographic film. The traces of rapid repetitive movements are resolved on the film by this technique into wave-like curves (Fig. 9) which are always easy to decipher. Taking the movement of the film into consideration (this can be done by means of very simple devices) and excluding it in calculations the observer can arrive at just as accurate and reliable data on the duration of movements from the curves obtained on the film as is available for the simplest movements from standard cyclograms.

3. Stereoscopic Recording of Movements

Both cyclography and kymocyclography give, in the applications described above, only the planar projection of the movement photographed. In order to examine movements in depth one must turn to complex observations. The displacement of any object in space, in other words changes in all three spatial coordinates of an object, must be recorded by observation from no fewer than two different points of view. Braune and Fischer photographed walking from 4 points simultaneously with separate independent cameras. Nowadays many investigators rely chiefly on stereoscopic cameras, i.e. cameras with two lenses with parallel optical axes. It is, however, easy to show that the accuracy of determination of the coordinate of depth is greater, the further apart are the two points of observation, in our case of both stereoscopic lenses. In standard stereoscopic cameras the lenses are 6·5 cm apart and the accuracy of measurement of the coordinate of depth is very low. It is necessary to separate the stereoscopic lenses a greater distance of the order of tens of centimetres. This separation results in gross differences in the fields of view of both cameras with parallel optical axes of the lenses. For this reason it is more convenient to photograph the movements with two cameras, and with the optical axes of the lenses convergent rather than parallel. This type of apparatus was employed by Drill [36]. For synchrony this author set the shutters of two cameras placed at some distance from each other on the same long axis. The Moscow biomechanic school selected another technique which is incomparably more accurate and convenient. The mirror method developed by the author [16, 18] allows one to obtain two distinct points of view with a single camera and thus only a single rotating shutter.

For this purpose a large plane mirror is placed in the field of view of a camera at a given angle to its optical axis. The mirror is set so that the moving object to be studied is visible twice in the field of vision of the camera, (a) directly and (b) reflected in the mirror (Fig. 10). The mirror replaces the second, distant point of view. If, for example, it is placed at an angle of 45° to the main optical axis of the objective, then the accuracy obtained is equivalent to the accuracy for convergent photographs with two cameras separated by twice the distance of the camera from the mirror. Strictly speaking, the accuracy of the photograph with the mirror is still higher

as here we need not worry about either the perfect matching of two lenses or the careful alignment of their two main axes which is of decisive importance for photography with two convergent cameras.

Material obtained with the help of mirror kymocyclography is in a class of its own in comparison with the accuracy which may be obtained by means of other existing techniques of recording movements. Kymocyclography allows one to obtain several hundred phases of a moment in a second, while measurement of the time intervals between successive phases may be carried out with the help of a strobometer with an accuracy of within one millionth of a second. Skilfully taken mirror kymocyclograms also give excellent spatial accuracy, to within not less than 1 mm on any of three mirror coordinates. However, the most important advantage of the technique just described in the most general terms lies in the ease with which the material obtained in this way can be subjected to quantitative analysis and to mechanical interpretation. Photographic registration of movements is in no way the final aim of investigation but merely its raw data, and thus permits an approach to the real goal of investigation—physiological and biomechanical analysis of the processes of movement.

Methods of Analysis of the Cyclogram. To decipher a cyclogram it is necessary in the first place to measure the photograph of the movement which we have obtained. It is exceedingly difficult to measure the positions of the cyclographic points directly on the photographic plate or film; moreover, such a process would in this case be very inaccurate. Fischer measured his negatives under a special microscope which is also inconvenient and insufficiently accurate because of the small field of view of the lens. The Moscow biomechanicians employ for this purpose a process of photographic measurement suggested by Lavrentiev. Cyclographical or kymocyclographical negatives are greatly enlarged, and during this process a millimetre or even a half-millimetre grid is transferred to the paper by the same photographic process. Then it is easy to calculate the coordinates of all cyclographical points with a high degree of accuracy (Fig. 11). These coordinates are the basic raw material to obtain which all the techniques that have been described above are necessary, and from the analysis of which it is now possible to extract the maximum available amount of information about the process of the movement which has been photographed. The inadequacy of the cinematographic method lies in the facts that it is

considerably more difficult to obtain these coordinates from a moving-picture film and that the degree of accuracy which can be attained is much lower.

All the cyclographical devices and procedures which have been described in this chapter have perforce been treated very briefly and superficially. The reader who wishes to acquaint himself more thoroughly with cyclogrammetrical processes may refer to Refs. 12, 16 and 18.

First of all it is necessary to establish from the coordinates obtained the successive positions in space occupied by the joints of the body from moment to moment during the time over which the cyclographical exposure was made (see Figs. 22 and 23(a)). Once a graph of these successive positions has been obtained, it is easy to measure the angles of articulation, repeating the process for all variations with their gradual changes. The coordinate data obtained from mirror kymocyclograms allow one to obtain all required projections of the successive stages of the movement under observation: to "see" it from behind, from the side and from above. This type of observation gives information about the whole extent or range of movements, the amplitudes of movements of particular points of the body, the limits of the changes of the angles of articulation, the distribution of the trajectories of the movements in relation to surrounding objects and the forms of these trajectories. The value and the practical importance of information of this type does not require further emphasis.

Changes in one of the coordinates of movements in time may be represented in the form of a curve. Such a curve describes with particular clarity the characteristic peculiarities of movements, their differences from other similar movements, symptoms of fatigue which appear in them, and so forth. These features are expressed more clearly in curves of changes in velocity of the movements which may also be obtained by very simple methods from data on the coordinates of movements. Curves of the angular velocities of the movements of joints may also be obtained with the help of simple techniques.

Analysis of the forces which produce a given movement is of great and sometimes decisive importance. The first steps towards the description of these forces by means of chronophotograms were made by Braune and Fischer who indicated the way in which calculations of this type might be made. It is impossible to obtain

direct data on these forces from chronophotographs or cyclograms. However, from these, and especially from the velocity curves which have just been mentioned, it is possible to obtain information on the acceleration of one or another point of the body. The dynamic forces are calculated by multiplication of the accelerations by the masses of the parts of the body undergoing acceleration. As will be apparent from the subsequent discussion, analysis of the forces producing movements and juxtaposition of these force data with data about the movements produced by operation of these forces gives a clear insight into the biomechanical and physiological characteristics of the processes of movement. The reader will see this for himself from the examples to be presented later.

4. Masses and Centres of Gravity of the Limbs of the Human Body

It is clear from the preceding discussion that it is possible to describe the work done by the skeletal musculature only if we have precise knowledge of the masses of the limbs of the human body and of the locations of their centres of gravity. Until recently this aspect of the problem was one of the most obscure in anatomy, and it is only now that an extensive investigation carried out by the author of this paper and his colleagues has in some degree begun to illuminate the problem of distribution of mass.

Two investigations of the problem indicated above are available in the literature; these are studies by Harless and by Braune and Fischer. These investigators employed the technique of dissection of frozen cadavers, following which the separate limbs were weighed and their centres of gravity determined by one of the methods of elementary mechanics. The number of cadavers used was extremely small; Braune and Fischer used 3 or 5 (the authors statements are contradictory), and the number used by Harless is unknown. The cadavers were those of adult males; there is no indication of their ages or physiques. The figures obtained from both studies are mean values without any indication of variation, and they differ significantly from each other (Tables 1 and 2).

It is already clear from the data presented here in brief that the material is inadequate. It is impossible to determine the most important facts of all—in what way these figures may be applied to a

TABLE 1. RELATIVE MASSES OF THE LIMBS
(MASS OF THE ENTIRE BODY = 1)

	Fischer	Harless
Head	0·0706	0·0712
Upper arm	0·0336	0·0324
Forearm	0·0228	0·0181
Hand	0·0084	0·0084
Thigh	0·1156	0·1118
Lower leg	0·0527	0·0439
Foot	0·0179	0·0183
Trunk	0·4270	0·4630

TABLE 2. THE DISTANCES OF THE CENTRES OF GRAVITY OF THE LIMBS
FROM THE PROXIMAL JOINT (LENGTH OF LIMB = 1)

	Fischer	Harless
Thigh	0·44	0·467
Lower leg	0·42	0·36
Upper arm	0·47	0·485
Forearm	0·42	0·44

given individual and in what ways they may vary for persons of different sex, age and body structure. Finally, they beg the most important question of all—to what extent the relationships that hold true for cadavers are characteristic of live subjects.

The primary obstacle to experimental analysis of all these questions has until recently been the complete absence of methods which would permit the necessary measurements to be made on living subjects. It appeared to be an impossible business to weigh a living human being, as it were, piecemeal. It was only after the author of this paper together with O. Salzgeber and P. Pavlenko solved experimentally the auxiliary problems which were most important for this purpose that it was possible to proceed to the study of the weights and the centres of gravity of the limbs of living subjects by employing the ideas of Scheidt and Hebestreit. It is impossible to present in this chapter even a brief account of the complicated and delicate method employed by the author and his colleagues for measurements of this type. It can only be said that the problem is ultimately related to the planimetric measurements of the volumes and volume moments of the limbs of the body and to

the weighing of the subject in numerous carefully determined controlled positions on special twin-support scales (see Fig. 12). From analyses of the figures obtained in this way and by comparison with data obtained from the most accurate microscopic examination of photographic plates of the positions assumed during the weighing, data on the locations of the centres of gravity of the limbs and on their masses could be obtained.

An analysis was undertaken of material obtained from 152 subjects of both sexes with an age range of 10–75 years. This study did not include investigation of the locations of the centres of gravity of head, hands or feet such as were determined by Braune and Fischer; rather, we investigated the locations of the centres of gravity of the upper arm, forearm, thigh and lower leg and the masses of all the major limbs of the body. The locations of the centres of gravity of the trunk and of the body as a whole were also included in the program of investigation.

I append below some of the data from the results we have obtained.

The mean values of the radii of the centres of gravity of the long limbs appeared to be much closer to those obtained by Fischer than to those by Harless (I term as the radius of the centre of gravity the distance from the centre of gravity to the centre of the proximal joint with the length of the limb taken as a unit). We may recall that Fischer's material was obtained on 3–5 subjects, while our material provides information on about 150 persons; because of this the reliability of the present data is many times greater than that of the old figures. I append a list of the means we obtained for comparison with those obtained by Fischer (Table 3).

TABLE 3. THE RADII OF THE CENTRE OF GRAVITY

	From our data		According to Fischer
	Mean value	Mean square deviation	
Thigh	0·3880	± 0·0332	0·44
Lower leg	0·4175	± 0·0224	0·42
Upper arm	0·4746	± 0·0338	0·47
Forearm	0·4145	± 0·0309	0·42

In the material as a whole, therefore, only in the case of the thigh does a significant difference from the position determined by Fischer

occur, but the second column of figures in Table 3 is of much greater importance indicating that the spread of the data, in other words the variation, is considerable. If we take the mean square deviation as a measure of the variation, it appears that the over-whelming majority of cases fall between the following limits.

Thigh	0·3548–0·4212
Lower leg	0·3951–0·4399
Upper arm	0·4408–0·5084
Forearm	0·3836–0·4454

These variations are comparatively insignificant. The deviations found with sex of subject, contrary to expectation, do not significantly affect the values of the radii obtained as Table 4 shows.

TABLE 4. RADII OF THE CENTRES OF GRAVITY OF THE LIMBS (IN MEN AND WOMEN)

	Men		Women	
	Mean value	Variations due to the mean square deviation	Mean value	Variations due to the mean square deviation
Thigh	0·3857	0·3543–0·4171	0·3888	0·3534–0·4242
Lower leg	0·4130	0·3942–0·4318	0·4226	0·3983–0·4469
Upper arm	0·4657	0·4394–0·4920	0·4840	0·4484–0·5196
Forearm	0·4124	0·3850–0·4398	0·4174	0·3835–0·4513

In the first place, it is apparent from this list that sex differences have very little effect on the radii of the centres of gravity. Generally speaking, the radii are slightly longer in women, that is, the centres of gravity lie closer to the middle of the limb and in the case of the upper arm they sometimes lie even lower which is almost never observed in men. In the second place, the indication in the first table of the great variation of the radii as encountered in practice is confirmed. Even if Fischer's figures, for example, those for the upper arm, closely coincide with our mean values (0·47 and 0·4746), it is possible to employ them in calculations, given the probability that for the overwhelming majority of subjects the values of the radius for the upper arm may vary in men between 0·44–0·49, and in women between 0·45–0·52. Figure 13 provides a picture of how the distribution of the values of radii of the forearm appear for men and women.

There are only two possible paths to choose in order to analyse this chaos of variations. Either we may resign ourselves to measuring with the complex techniques we have developed every new subject with whom we deal—or we may attempt to find such anthropometric and structural correspondencies (correlations) as will enable us to determine with sufficient accuracy the probable radii of our subjects on the basis of their general habitus and anthropometric data. It was this latter which we set as the objective of our investigations.

If we now turn to the masses of the limbs of the body, we may say that in this respect the data of Fischer and Harless were even more unreliable. The massive sample of material we examined gives an entirely different picture,* even if we consider only the mean values obtained quite independently of any variation (Table 5).

TABLE 5. RELATIVE MASSES OF THE LIMBS (MASS OF THE BODY AS A WHOLE = 1)

	Our Data				Mass according to Fischer
	Men	Women	General mean	Ratio M/W	
Thigh	0·12213	0·12815	0·12485	0·948	0·1158
Lower leg	0·04655	0·04845	0·04731	0·961	0·0527
Foot	0·01458	0·01295	0·01313	1·126	0·0179
Upper arm	0·02655	0·02600	0·02632	1·021	0·0336
Forearm	0·01818	0·01820	0·01819	1·000	0·0228
Hand	0·00703	0·00550	0·00642	1·279	0·0084

The following interesting circumstances may be observed from Table 5. In the first place Fischer greatly overestimated figures for all the extremities of the limbs except the feet. In fact, the masses of all these extremities of the limbs are much smaller than is represented by these figures, which have been for 40 years the only data available on the question of the distribution of masses in the human body. In the second place, we here observe significant and characteristic differences between the sexes. The column giving the ratio of the mean masses illustrates these differences most clearly. Male thighs are significantly lighter than female thighs and lower legs and upper arms are almost the same for men and women (it

* The figures given here are only preliminary and after final revision may undergo small changes.

should not be forgotten that in all these cases we are discussing relative masses, that is to say masses estimated with the total body weight taken as the unit); but distal portions of the limbs in men are significantly heavier than those of women. Both for the legs and for the arms the ratio M/W shows an increase from the proximal to the distal end of the limbs becoming particularly significant for the feet (13 per cent) and for the hands (28 per cent). It is also necessary to determine variation in the relative masses of human limbs. So as not to enter into complications we give only a general table which illustrates this considerable variation (Table 6).

TABLE 6. THE VARIANCE OF THE RELATIVE MASSES OF THE LIMBS (THE VALUES ARE GIVEN IN HUNDRED-THOUSANDTHS OF THE WEIGHT OF THE WHOLE BODY AND IN PERCENTAGES OF THE MEAN MASS OF THE LIMB)

	Men		Women		General figure	
Foot	1620	±13·3%	±1190	± 9·2%	±1480	±11·8%
Lower leg	507	10·9%	389	8·0%	469	9·9%
Thigh	126	8·6%	105	8·1%	142	10·2%
Upper arm	312	11·8%	344	13·2%	322	12·2%
Forearm	184	10·1%	169	9·3%	177	9·7%
Hand	84	11·9%	98	17·8%	117	18·2%

The variation both in the radii and in the relative masses is least for the lower legs, feet and forearms; the masses of the thighs, upper arms and in particular of the hands display greatest variance.

The Centre of Gravity of the Entire Body and of the System as a Whole. If the masses and the positions of the centres of gravity of all the separate limbs of the body are known, the problem of discovering the centre of gravity of the whole body or of any particular system (for example, that of the whole arm or of the whole leg) presents no difficulty whatever. This possibility is of inestimable importance for the physiology of movements because it opens the way to the dynamic analysis of the movements of the whole body and of its sub-systems and also allows us to study the statics of the body and, as has been explained above, the loads on any given group of muscles.

CHAPTER II

THE PROBLEM OF THE INTERRELATION OF CO-ORDINATION AND LOCALIZATION

### 1. The Basic Differential Equation of Movements

The relationship between movements and the innervational impulses which evoke them is extremely complex and is, moreover, by no means univocal. I have already undertaken an analysis of this relationship in a series of previous studies [8, 9, 14, 15] and for this reason I shall present here only a short summary of such statements as may be regarded as firmly established at the present time. The main object of this summary is to serve as an introduction to a further discussion.

The degree of tension of a muscle is a function, in the first place, of its innervational (tetanic and tonic) condition E, and, in the second place, of its length at a given instant and of the velocity with which this length changes over time. In an intact organism the length of a muscle is in its turn a function of the angle of articulation α; for this reason we may write that the momentum of a muscle with respect to the joint is

$$F = F\left(E, \alpha, \frac{d\alpha}{dt}\right). \tag{1}$$

On the other hand, we may assert that the angular acceleration of a limb controlled by a given muscle is directly proportional to the momentum of the muscle F and inversely proportional to the moment of inertia of the limb I. In this way

$$\frac{d^2\alpha}{dt^2} = \frac{F}{I}.$$
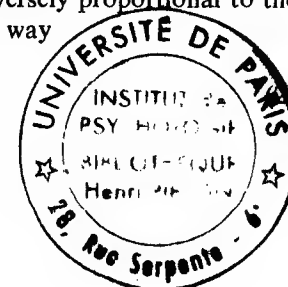
If there are other sources of force than the muscle operating on the limb, the situation is a little more complicated. Let us limit ourselves for simplicity to only one external force, namely gravity. In the simplest case which we have just described, where we are considering the movement of a single limb segment in relation to a second fixed one, the momentum due to gravity G is, like the momentum of the muscle, a function of the angle of articulation

$$G = G(\alpha). \tag{1a}$$

The angular acceleration of the limb segment under the influence of both momenta together is expressed by the equation

$$\frac{d^2\alpha}{dt^2} = \frac{F + G}{I}.$$

If we introduce into this equation expressions (1) and (1a) for F and G, we obtain a relation of the following form:

$$I \frac{d^2\alpha}{dt^2} = F\left(E, \alpha, \frac{d\alpha}{dt}\right) + G(\alpha). \tag{3}$$

This is the fundamental equation for the movement of a single limb in a gravitational field under the influence of a single muscle where the level of innervation is E. In cases where the moving system consists not of one but of several limb segments and where we are obliged to take into consideration the activity of several muscles, eqn. (3) becomes extremely complicated, not only quantitatively but also qualitatively as considerations of the mechanical effect of one muscle upon others also enter into the problem and the moment of inertia of the system becomes a variable term. However, in spite of the fact that the complications which arise in this case are so great that equations of type (3) cannot always be written even in the most general form, the physiological aspects of the problem differ only slightly, and the complications essentially involve only the mathematical and mechanical aspects of movement. For this reason in the present context we may limit ourselves only to the consideration of the most simple equation (3).

This basic equation is a differential equation of the second order which may be integrated if the functions F and G are known. Solutions of an equation of this type, that is to say, the determination of the movement which will take place in each given case, will be
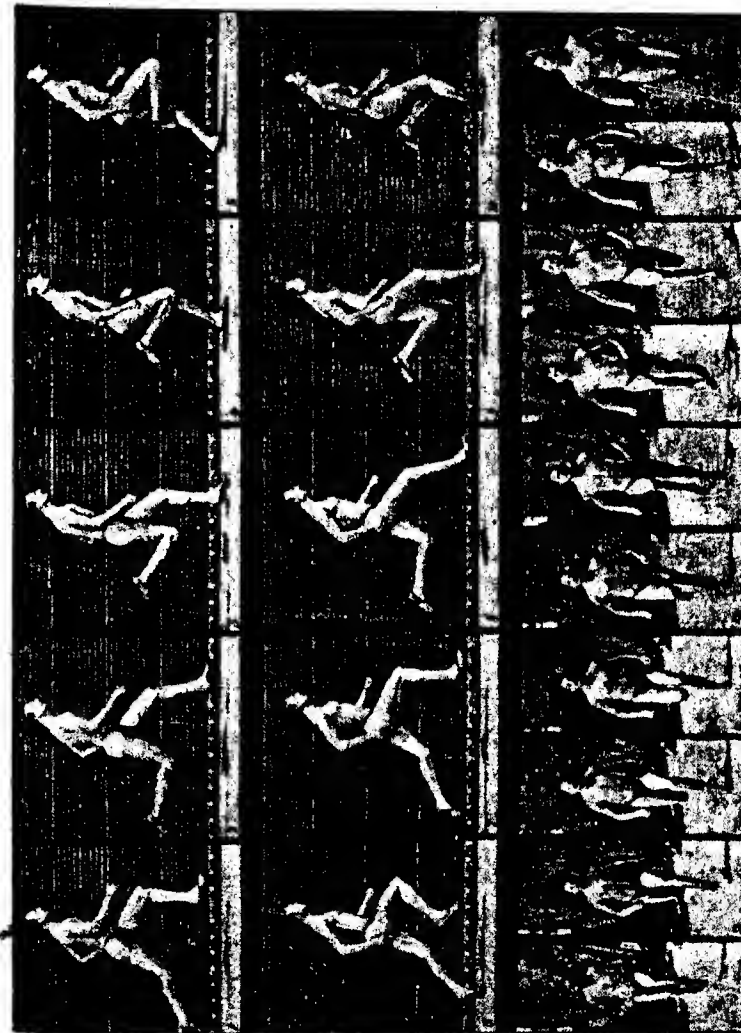
FIG. 1. Instantaneous photographs of running taken by Muybridge in the 1880's at the dawn of instantaneous photography. The time interval between successive frames is $^1/_{24}$ sec.

FIG. 2. One of Marey's subjects in a black costume with white tape.
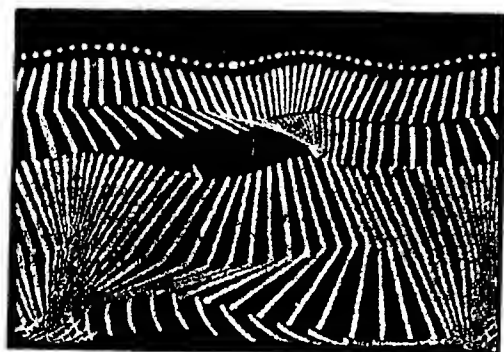
FIG. 3. Chronophotograph of walking taken by Marey. Movement is from left to right. The frequency is about 20 exposures per sec.

FIG. 4. Chronophotograph of walking taken by Braune and Fischer. Right side of the body; movement is from left to right. The square in the centre of the picture is a superimposed scale. Frequency—26 exposures per sec.
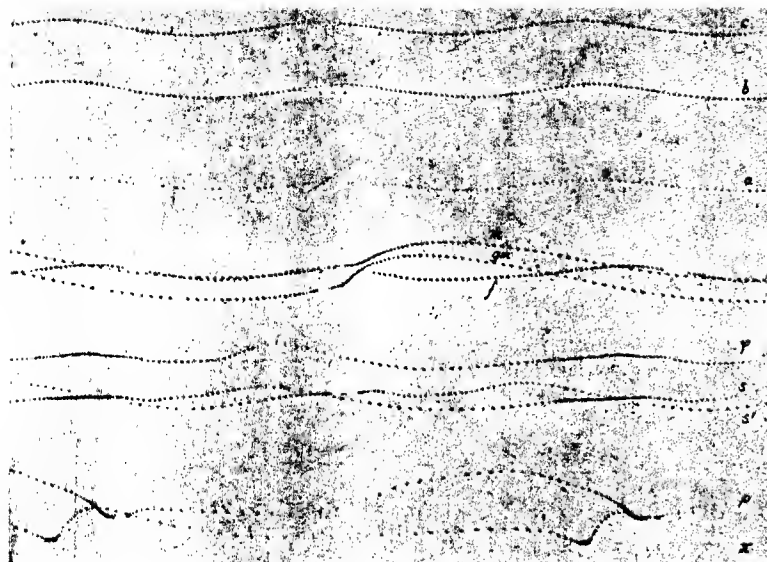
FIG. 5. Cyclogram of walking (Bernstein and Popova). Left side of the body; movement is from right to left. Trajectories from top to bottom: c, centre of gravity of the head; b, shoulder joint of the left arm; a, elbow joint of the left arm; m, radial side of the wrist joint of the left hand; gm, centre of gravity of the wrist; f, hip joint of the left leg; φ, a point on the longitudinal axis of the left thigh; s, knee joint of the left leg; s', knee joint of the right leg; p, ankle joint of the left leg; π, a point near the end of the foot. Frequency—90 exposures per sec.
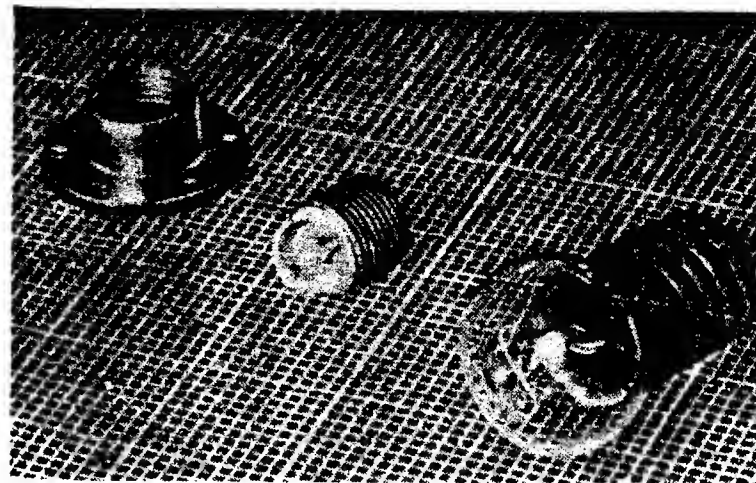

FIG. 6. Bulbs used for cyclography, placed on a millimetre grid so that their dimensions may be gauged. (Left) a Wolf socket; (centre) a Wolf–Bernstein bulb; (right) for comparison, the type of bulb commonly used in pocket flashlights.
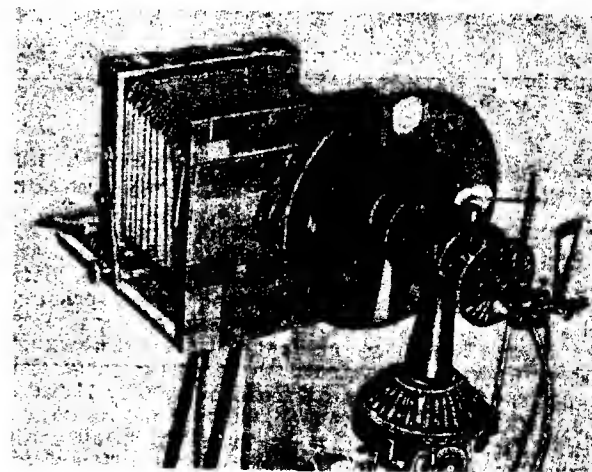
FIG. 7. Camera with rotating shutter, equipped with a siren so that its velocity of rotation may be estimated. In a later system used by the author the rotating shutter is semi-transparent; this provides faint lines on the cyclogram, uniting successive points on the same trajectory.
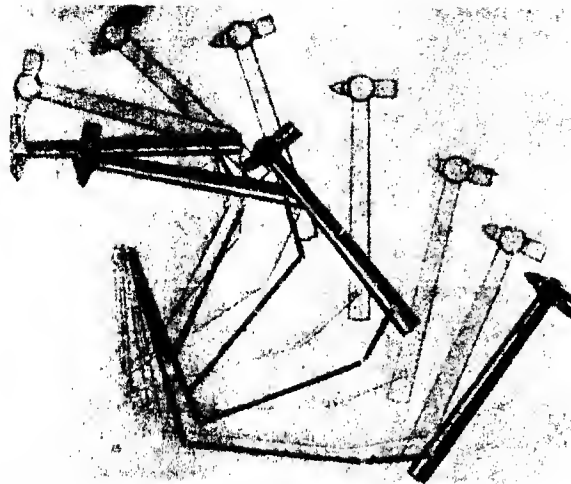
Fig. 8. Successive positions of the right hand and a hammer during correct striking with a chisel. The time interval between each phase shown is $^1/_{15}$ sec. The sketch was made from a cyclogram.
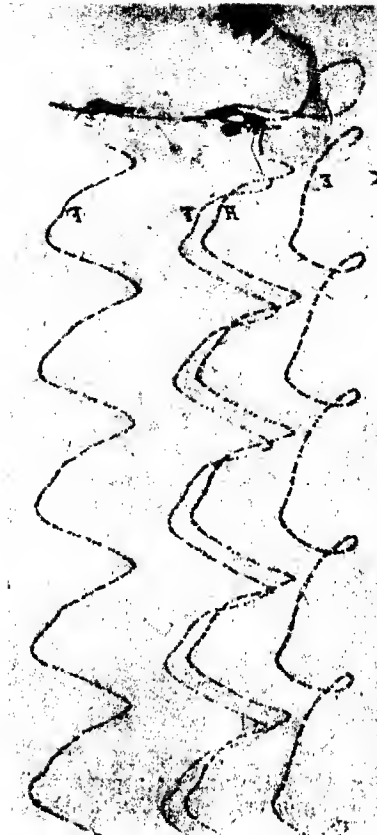
Fig. 9. A kymocyclogram of filing. The figure of the subject is visible at the top of the illustration, with a standard cyclogram of a single cycle of the movement of filing. This can be seen to be quite unanalysable. Below is a series of curves of the same movement, separated by being photographed on a moving film. K, a control bulb; E, the elbow joint; H, the radial side of the wrist joint; F, the fingers of the right hand; F', the fingers of the left hand. Frequency—73 frames per sec (1923).
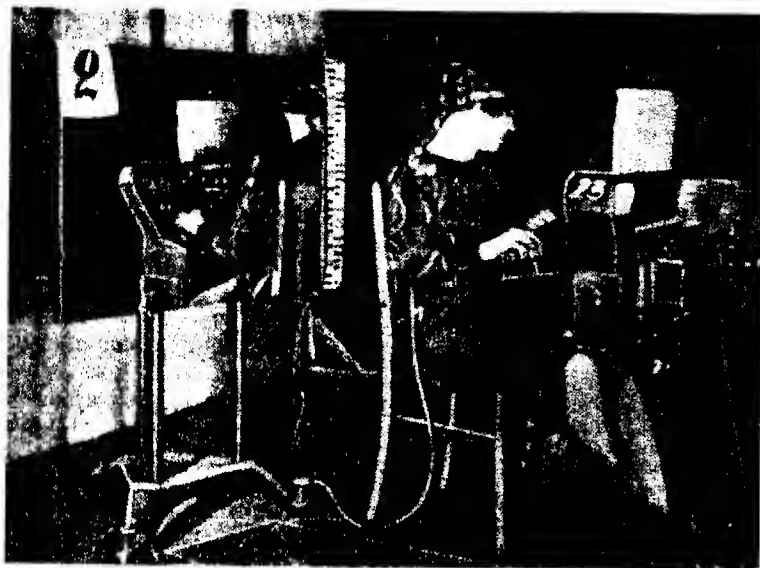
FIG. 10. Apparatus for mirror kymocyclography. The subject is operating a Powers perforator. On the left we have a mirror with a scale and the serial number (1929).
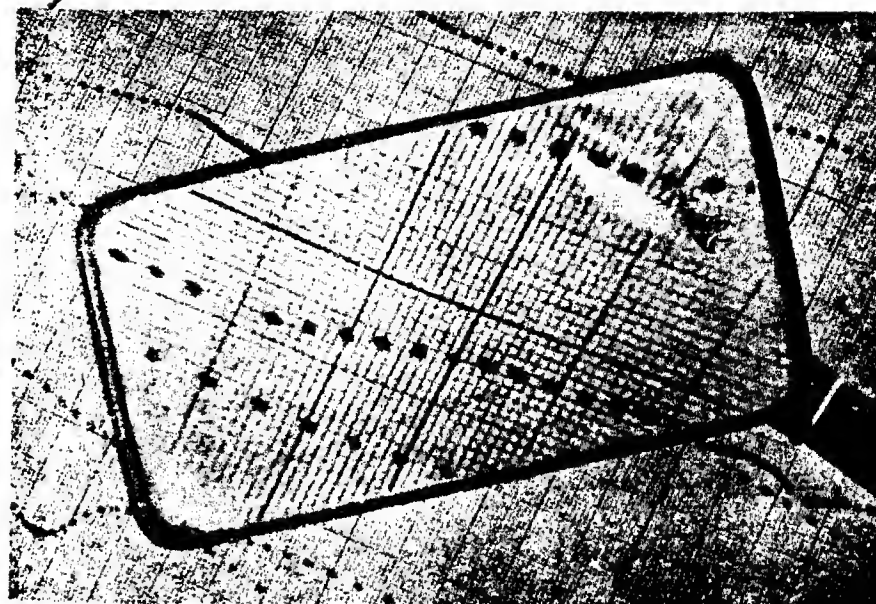
FIG. 11. A section of a photograph on a measuring grid and the means by which it is studied through a lens.
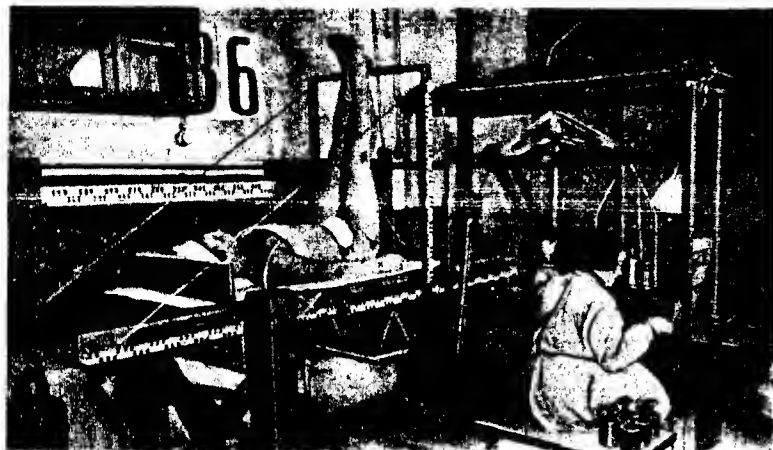
FIG. 12. An experiment on the determination of masses and the centre of gravity of the limbs by Bernstein's method. The subject lies in a predetermined position on a platform supported at two points, the placement of the head and the lower extremities being determined by upright boards. At the end the platform is fixed upon a fulcrum, at the lower extremity it is supported by one of the pans of accurate scales. The asssistant balances the static moment of a given position of the scales, the position being photographed at the same instant on a predetermined scale.
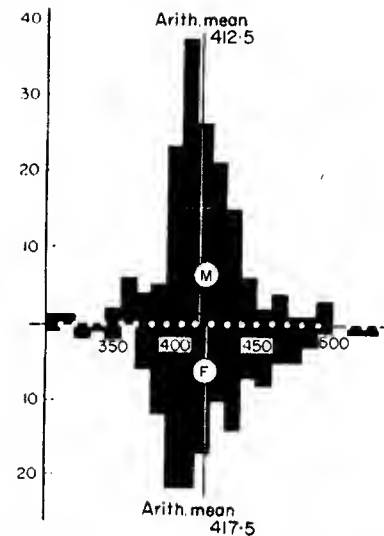
FIG. 13. Distribution of the values for the radii of the centres of gravity of the forearm from data obtained by the author and his colleagues. Above: the limits for men; below: those for women. The values of relative radii are plotted along the abscissa. The number of cases observed is plotted along the ordinate.

different depending on the so-called initial conditions of integration: that is, the initial position of the limb segment determined by the angle α_0 and on its initial angular velocity $d\alpha_0/dt$. By altering these initial conditions in various ways we may obtain very different effects of movement from one and the same governing law (3), i.e. for the same functions F and G.

It must first of all be noted that eqn. (3) directly bears on the cyclical character of the relation between the momentum of the muscle F and the position of the limb α. The limb segment changes its position as a result of the operation upon it of the momentum of effort F and this momentum in its turn changes because of the changes in the angle α. A cyclical chain of cause and effect operates in this way.

This chain would be ideally cyclical if the momentum (eqn. (1)) depended solely on α and $d\alpha/dt$, that is, if the movement were completely passive (for example, the falling of the arm). But, as in eqns. (1) and (3) given in this report, the value of F also depends on the degree of excitation of the muscle E, which appears most clearly from the areas lying outside the circle which we have just described. It is apparent that there are two possibilities here; either the degree of excitation E depends wholly or partly on the values of α and of $d\alpha/dt$, or it is quite independent of them and is solely a function of time t.

The choice between the two possibilities indicated here is clearly of great physiological significance as may be revealed with sufficient clarity only by further discussion in this chapter. At the moment I shall only indicate some of the consequences of each of the hypotheses we have raised.

If the degree of excitation E is simply a function of position and velocity and not a function of time, then eqn. (3) will take the form of a classic differential equation,

$$ I\frac{d^2\alpha}{d^2t} = F\left[E\left(\alpha, \frac{d\alpha}{dt}\right), \alpha, \frac{d\alpha}{dt}\right] + G(\alpha), \qquad (3a) $$

the partial integrals of which depend only on the initial conditions. In this case, consequently, a movement must occur if the required initial conditions are fulfilled (from without), and once having begun it must proceed with the same uninterruptable regularity with which a string will oscillate if displaced to a precisely determined initial position and then released. It is clear that this hypothesis does not

correspond to physiological reality and in effect completely ignores the role of the central nervous system.

On the other hand, it may be supposed that the degree of excitation E is a value which changes with time and depends entirely on a predetermined sequence of impulses from the central nervous system without any relation to the local conditions operating in the system of the moving limb being studied. If, as in the hypothesis formulated above for the elastic oscillation of a string, the muscle can be compared to some sort of independent spring or rubber band, then in the second hypothesis it may be represented as a sort of solenoid which attracts its core solely in relation to the potential of the current which is supplied to the coil from an external source. The law of the variation in this current must be represented in the system of eqn. (3) as a function of time; in fact, whatever may be the real causes of these changes, the changes themselves are presented to system (3) in a completely finished and independent form as quite unalterable data. Equation (3) in this case takes on the form

$$I\frac{\mathrm{d}^2\alpha}{\mathrm{d}^2 t} = F\left[E(t), \alpha, \frac{\mathrm{d}\alpha}{\mathrm{d}t}\right] + G(\alpha),\qquad(3\mathrm{b})$$

which does not permit of any concrete solution.

It is important here to draw attention to the following. In spite of the fact that the degree of excitation E, as has been hypothesized, is independent of α and of $\mathrm{d}\alpha/\mathrm{d}t$, the momentum of the muscle F is dependent on them as before. Meanwhile, as we have shown above, the operation of this momentum, that is, the entire picture of the course of a movement, will vary with the initial conditions which in no way enter into the expression for the degree of excitation E and consequently do not in any way affect the course of its changes in time. It follows from this that the general results of interactions from eqn. (3b) cannot be foreseen or regulated in advance because the changes in excitation will be involved in the interplay of forces and dependencies which can in no way alter the further course of these changes following a fully independent law. Movements which are regulated according to the law (3b) will necessarily be ataxic.

And so we are left with the hypothesis that the excitation of a muscle E must be both a function of time and a function of position

and velocity, and must be described in eqn. (3) in the form

$$I\frac{\mathrm{d}^2\alpha}{\mathrm{d}t^2} = F\left[E\left(t, \alpha, \frac{\mathrm{d}\alpha}{\mathrm{d}t}\right), \alpha, \frac{\mathrm{d}\alpha}{\mathrm{d}t}\right] + G(\alpha).\qquad(3\mathrm{c})$$

This purely analytical deduction of the functional structure of muscle excitation permits of exceptionally simple translation into physiological terms. The dependence of the variable E on time, proceeding from the absurdity of the opposite hypothesis (3a), underlies the necessity for the changes in excitation which are directly effected by the activity of the motor areas of the central nervous system. The dependence of the excitation on the position of the limb α and its angular velocity $\mathrm{d}\alpha/\mathrm{d}t$ is the proprioceptive reflex so well known in physiology. It necessarily follows from the preceding analysis that both position and velocity directly and independently influence the changes in the degree of excitation of the muscles, and in reality both these effects have been subjected to precise physiological investigation.

Turning to clinical evidence we may say that (3a) is the equation of movement for an extremity in a case of central paralysis and that (3b) represents the equation of movement in a case of proprioceptive ataxia.

In this way we have stated in the basic equations of movement a superposition of two cyclical connections of different orders and related to different topics. The first cyclical connection is the mutual interaction of the position α and the momentum F, and exists purely mechanically as has been pointed out above. The second connection constructed on the first one, is a similar interaction between the position α (and also of the velocity) and the degree of excitation E; this connection is effected by means of systems of reflexes and is related to the activity of the central nervous system.

The principal significance of the general conclusions examined above may easily be deduced. The customary older representation implicitly accepted and, until the present, retained by many physiologists and clinicians, describes the skeletal link as being completely passive under the control of the central impulses and as being unequivocally subservient to these impulses. In this scheme the central impulse a always produces movement A, and impulse b always produces movement B, from which it is easy to proceed to a representation of the motor area of the cortex as a distribution panel

with push-buttons. However, eqn. (3b) indicates that one and the same impulse $E(t)$ (ignoring the periphery) may produce completely different effects because of the interplay of external forces and because of variations in the initial conditions. Equation (3c) shows, on the other hand, that a determinate effect is possible for a movement only in a case where the central impulse E is very different under different conditions, being a function of the positions and the velocities of the limbs and operating very differently in the differential equation with various initial conditions. Parodying the well
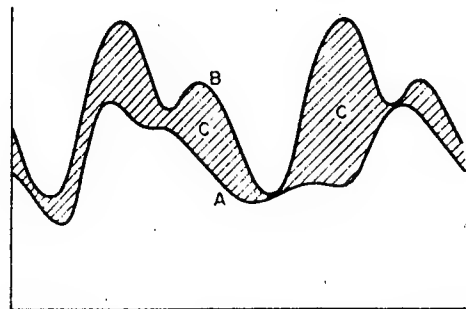

FIG. 14. A semi-schematic representation of the course of a single central impulse during a rhythmical movement. A, the non-rhythmical curve of changes in external forces; B, the summed rhythmical result; C (hatched area), an impulse bridging the gap between the curve A and the result B.

known tag on nature we may say that *motus parendo vincitur* (movement is conquered by obedience).

It must be pointed out, finally, that the external force field does not consist of the force of gravity $G(\alpha)$ alone and it may even occur that this latter expression does not enter at all into the basic equation in such a simple form. Because it necessarily affects the position and the velocity of a system, and because in the norm these latter affect the changes in E, we may say that the *parendo* of the central impulses must sometimes go to great lengths. It is obliged to adapt to all internal and external forces operating in the system·while forces which do not directly depend on the operation of the impulse E may frequently play a decisive part in the general balance of forces affecting movement. In such cases (Fig. 14), if for a given movement the required changes of forces at the joint are represented by the curve B and the resultant forces in the external field are represented

by the curve A, then the central nervous system will be obliged to provide only the additional fraction C so that the sequence of impulses cannot maintain even a remote correspondence to the contours of curve B and frequently even less correspondence with this curve than to the changes in the external field A. These supplementary compensatory impulses sometimes appear in an indirect way from cyclogrametric observation.

And so, not to enter into details discussed in the studies mentioned above, it may be said that:

(a) a unequivocal relationship between impulses and movements does not and cannot exist;

(b) the relation between impulses and movement is the further removed from unequivocality the more complex is the kinematic chain operating in the movement under consideration;

(c) movements are possible only under conditions of the most accurate and uninterrupted agreement—*unforeseen in advance*—between the central impulses and the events occurring at the periphery, and are frequently quantitatively less dependent on these central impulses than on the external force field.

2. The Integrity and Structural Complexity of Live Movements

In the treasury of experimental physiology there are vast collections of experimental observations and facts characterizing the course of single impulses or of the more simple patterns of impulses. There are most detailed studies of all aspects of excitation, inhibition, *parabiosis, chronaxie*, and so on, for a single nerve pathway. However, we have up to the present only two major advances along the lines of investigation of the total or systemic operation of impulses: Sherrington's principle of reciprocity and A. Ukhtomskii's principle of dominance. But even these groups of data are very far removed from the areas we touch upon—the problems of the study of structures of movements as integral formations.

It is, however, precisely this integration of movements that is the most important feature implied by "motor co-ordination". The fact of this integration may be investigated in many experimental situations and significant connections and correlations are observed in all these cases between the various components of the integrated

processes. The simplest and most easily observed phenomenon in this category is the appearance of gradual and smooth redistribution of tensions in muscular masses, which is particularly clearly expressed in cases of phylogenetically ancient or highly automatized movements. A muscle never enters into a complete movement as an isolated element. Neither the active raising of tension nor the concomitant (reciprocal) inhibition in antagonistic* subgroups is, in the norm, concentrated in a single anatomical muscular entity; rather,
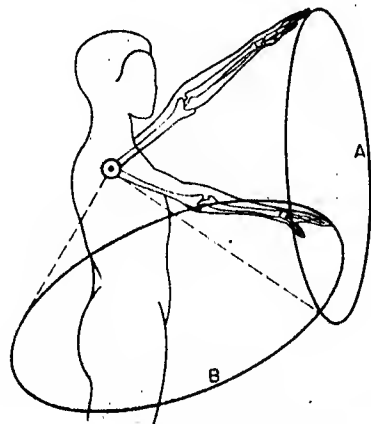

FIG. 15. Circular movements made with the arm extended in various positions are accomplished by completely different innervational schemes for trajectories of the same type.

there is a gradual and even flow from one system to others. I shall suggest a short experiment; stretch the arm out anterolaterally and describe a great circle with the hand as shown in Fig. 15, and then find out by means of anatomical analysis how the change in muscular innervation and the process of inhibition of the antagonists are accomplished during this movement. Exactly the same process of gradual transfer of innervation may be clearly observed in any

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* The concept of antagonism may be applied unconditionally only to cases of muscles operating on joints with a single axis and, further, to those which cross only this one joint. The number of muscles of this type is extremely small; in the skeletal extremities we find as examples of this type only m. brachialis internus, m. pronator quadratus, the short portion of m. triceps brachii and m. vastus femoris. All other muscles may be only functionally antagonistic in a single situation and in quite different relationships in other situations.

plastic movements; with more accurate means of registration this may be observed as a general phenomenon.

The integration discussed above is even more clearly demonstrated in the analysis of automatic rhythmical movements by the appearance of extremely marked reciprocities in the interrelationships of the components. I have described examples of such reciprocity in other studies [9, 19]; I shall here merely refer to the fact that in rhythmical work with a hammer the direction of the trajectory of the elbow (forwards or to the side) gives a close correlation with such phenomena apparently far removed from the elbow as the relationship of the maximal velocities of the head of the hammer in the movements of raising and striking, the angle of inclination of the hammer to the horizontal in raising, the relationship between the length of the trajectories of the hammer and of the wrist, and so on. It seems to me that the effects of changes in tempo on the whole construction of a movement are relevant here, as I have discussed in other studies [14, 19] on striking piano keys and on locomotion. A movement never responds to detailed changes by a change in its detail; it responds as a whole to changes in each small part, such changes being particularly prominent in phases and details sometimes considerably distant both spatially and temporally from those initially encountered.

Finally, it is necessary to comment on a fact to which I have drawn attention in a number of places [14, 15, 19, 21]; that the course of rhythmical live movements may be represented in the form of rapidly converging trigonometric series. I have been able to demonstrate that a diversity of rhythmical human movements (walking, striking with a hammer, filing, piano-playing, etc.) may be interpreted to an accuracy of within a few millimetres in the form of a sum of three or four harmonic oscillations, the so-called Fourier trigonometrical sums:

$$r = A_0 + A_1 \sin \frac{2\pi}{T} (t + \theta^1) + A_2 \sin \frac{4\pi}{T} (t + \theta^2)$$

$$+ A_3 \sin \frac{6\pi}{T} (t + \theta^3) + \cdots \tag{4}$$

The rapidity of convergence of these sums may be seen from the numerical examples of Table 7.

TABLE 7

Walking	Absolute amplitudes				Relative amplitudes ($A_1 = 100\%$)		
	A_1 cm	A_2 cm	A_3 cm	A_4 cm	$A_2\%$	$A_3\%$	$A_4\%$
Longitudinal displacement of the point of the foot	38·50	9·09	0·80	0·67	23·6	2·08	1·74
Longitudinal displacement of the centre of gravity of the whole arm	7·60	0·81	0·15	0·07	10·65	1·98	0·92
Longitudinal displacement of the center of gravity of the whole leg	14·47	1·22	0·49	0·22	8·42	3·39	1·52

The fact that such an interpretation is possible is of great importance to the question under discussion. If one complete cycle of a movement lasts for 1 sec, and in this case may be represented with an accuracy of within 1–3 mm as the sum of three sinusoids, this means that all the details of this movement must have been organized with the required degree of accuracy a full second beforehand. Further, its period being known, the sinusoid is determined by two parameters, that is, it can be determined from two points. The sum of four sinusoids may thus be theoretically determined from eight points; in other words, it is possible to reconstruct from a small section of a movement of the type which we have represented, to within a fraction of one per cent in the form of the sum of four sinusoids, the entire movement as a whole with the same order of accuracy. This experimental fact is evidence in its most cogent form of the organizational interaction and mutual reciprocity of rhythmical movements in time, while the mutual interdependence between the elements of the movement which I studied (of striking with a hammer) suggests a similar interaction in terms of spatial components.

If the external expression of co-ordinational activity provides a picture of such a high degree of reciprocity and interrelatedness, then, on the other hand, its anatomical structure in terms of our present knowledge also displays a picture of no less highly organ-

ized complexity. The extreme variety of clinical studies of damage to the motor area suggests that a large number of different subordinate and variously interacting systems co-operate in order to make possible a movement in its entirety. The spinal system alone contains up to five independent centrifugal pathways (pyramidal, rubrospinal, vestibulospinal and two tectospinal pathways). In the cortical region we have a very large number of centres which in one way or another appear (most often from pathological evidence) to be necessary components in a complete movement. All attempts to describe their activity in the norm are necessarily limited at the present time to very general statements and hypothetical descriptions, but there is no doubt whatever of their synthetic activity. For example, the attempts of Bianchi, Brown, Dupré, Foerster [44], Goldstein, Gurevitch, Homberger, Jacob, Lashley, Lewy [52], Magnus [55], v. Monakow [59], and many other investigators to describe in one way or another the functional interactions of various parts of the cortex must be mentioned here with recognition of the great service these authors have rendered to the physiology of movement.* A brief summary of what these authors have uncovered in areas directly bearing on the objectives of this report would be approximately as follows. An impulse reaching the terminal plates in a muscle from the centrifugal fibre of the last neuron is the resultant of a whole series of separate central impulses which reach the synapses of the anterior horn by different pathways. Among these latter we must recognize the significant innervational independence of pyramidal impulses (the cortico-spinal tract) and the combined impulses from the striopallidal groups of nuclei (c. striatum–gl. pallidus–nucleus ruber–tr. rubro spinalis) which are found in close co-operation with centres spinalis) whose functional relationships are less apparent (substantia nigra, Dark-schewitsch's nucleus, corpus Luysi, and so on). Centripetal proprioceptive impulses give rise to answering effector impulses from the cerebellum and from other many stations related to the spinal cord through the quadrigeminal system. Finally, the de-

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* Bianchi, *The Mechanism of the Brain*, etc., Edinburgh, 1922; T. G. Brown, *J. Physiol.* 10, 103; Dupré, *Revue neurol.* 1909, p. 1073, 1910, No. 13; K. Goldstein, *Deutsche Ztschr. Nervenheilk.* 70, P, p. 7; M. Gurevitch, *Ztschr. ges. Neurol. Psych.* 93, 1924; *Ibid.* 108, 1927; Homberger, *Ztschr. ges. Neurol. Psych.* 85, and *Arch. f. Psychiatrie* 69; Jacob, *Ztschr. ges. Neurol. Psych.* 89; K. S. Lashley, *Brain* 41, 255; *et al.*

cisive role in the production of a movement must be referred not to a centrifugal but to a central-informational system (an older physiology would have termed this "commissural-associative") interplaying along the lines of the frontal pontocerebellar pathways. It would be possible to list the general characteristics of the functional peculiarities of each of these anatomical stations (often the details given by different authors are contradictory), but this is not my aim at present. It is important here to point out a single peculiarity which is common to all these characteristics and which has been stated as an undisputed fact for the last 20 years.

All the clinical observations noted above, as well as those of many other authors, agree on the position (quite foreign to the ideas of other physiologists of the last century) that these central nervous sub-systems have one and the same object of excitation at the periphery—the same muscles and most probably the same peripheral conducting pathways. The idiosyncracies and differences in the operations of the pyramidal, striopallidal, cerebellar, and other systems lie not in differences and peculiarities in the peripheral objectives on which they operate but solely in differences in the forms of influence exercised on these objectives. The pallidum is concerned with the same musculature as is the brain cortex; it is not the objective but the manner of excitation which is specific. None of the data from contemporary physiological investigations contradicts the reliability of the fact that, for example, both flexion and extension in any single-axis joint can be achieved through both pyramidal and the striopallidal systems; both these systems may and do give the effect of reciprocity. In "gross pathology" this is carried out separately and in the healthy norm both systems in some way co-operate in a rhythmical process. As accounts of the way in which this co-operation may be effected we have in the literature many observations, impressions, and deliberations which are often quite persuasive and in many cases not contradictory. What is common to all these descriptions is not in general important; what is important, with the object of a formal examination of material, is the general tendency found in all of them—the recognition of the common presence in all cases of the qualitatively peculiar operation of central subsystems on one and the same peripheral objects.

Closely related to these considerations is the currently established picture of the multiplicity of projections of peripheral organs in the central nervous system. Along the lines of the exceptionally detailed

knowledge of cortical projection of the motor periphery, which was already under investigation in the 19th century, and which has been worked out in very great detail in our time (Fig. 16), we are now obliged to hypothesize localized projections of the same periphery both on the globus pallidus and on the cerebelli vermis. It is immaterial to our purpose in what way this multiplicity has occurred as a result of phylogenetic stratification and superimposition. In the human being, it is presented to us as given data, a given problem, and our task lies in the search for non-contradictory explanations of the mechanisms of a multistaged functioning of this sort.

If we attempt an examination from the point of view of such multiplicity of the equations for elementary movements (3c) which we have deduced above, we necessarily arrive at the following. A nerve impulse E, which, as appears on close examination of peripheral processes, is not related in a univocal way to its consequence —a movement—and is therefore restricted to the most precise concordance between its evolution and the proprioceptive input for α and $d\alpha/dt$, is at the same time the sum of (or is in some other form of linked equivalence to) a series of impulses which have very differ-
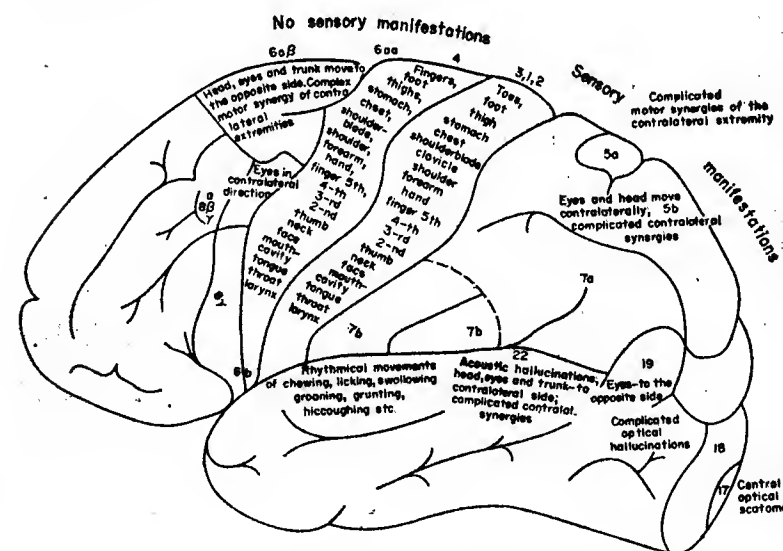

Fig. 16. Summary of data given by O. Foerster on results of stimulation of various points of the human cortical hemisphere (1926).

ent points of origin in the brain. Each of these impulses arises in a separate area in the brain that is distinct from other centres. Each of these centres has its particular interrelationships with other centres in the brain, its own conducting pathways, a particular degree of relationship with and form of connections to the receptors, and, finally, as clinical practice in nervous disorders shows, its own mode of operation in time and its own particular means of interaction. The difficulty of co-ordinating all these facts is very great indeed as I shall attempt to demonstrate. If the impulse E were to follow the pattern in eqn. (3b), that is to say if it had the form $E(t)$, it would not in principle be difficult to represent a series of independent sources (a very high degree of agreement between them being implied) which would ultimately unite in a single common path of a motor nerve and transmit the result of their common action $E(t)$ through it to the end plate. In exactly the same way it would not be difficult to conceive of the possibility of multiple action of impulses in a case where the actual form was (3c), that is, $E(t, \alpha, d\alpha/dt)$, if each of the separate impulses had its own particular object of excitation at the periphery (in the form, for example, of a particular muscle which was controlled by it alone). If we suppose, for example, that control of a flexor group at a joint is concentrated in the centre A and control of the extensor group of the same joint in centre B while the proprioceptive connections secure the possibility of either centre being able to react to α and to $d\alpha/dt$, then the mechanism in this case would be merely quantitatively and not qualitatively difficult to comprehend. The actual situation—that is, a system of impulses without unequivocal correspondence to the movement, and controlled by proprioception, being sent to the object from a number of sources—is one which does not permit us any simple escape from the question. The sole (apparent) possibility of explanation for a structure of this type lies in referring the proprioceptive "perception" to only one of the effector centres of the brain, for example, to the cerebellum, and supposing that the other effectors function purely according to type $E(t)$. The mathematical expression of such a structure might be regarded in the following way: the summed impulse E is made up of a series of central impulses $E_1, E_2, E_3, \ldots$

$$E\left(t, \alpha, \frac{d\alpha}{dt}\right) = E_1(t) + E_2(t) + \cdots + E_n\left(\alpha, \frac{d\alpha}{dt}\right). \quad (5)$$

However, this combination appears to be unacceptable for a number of reasons. In the first place, we have no guarantee whatever that E is the sum of $E_1, E_2, \ldots, E_n$, and not some other function of them such as would considerably alter the case and complicate for the co-ordination centre E_n the possibility of suppressing the "blind" impulses E_1, E_2 with precisely proportional additions. In the second place, the centripetal impulses are directed in the spinal cord not through one channel, but through a large number of channels, and reach by direct pathways at least two central nuclei, cerebellar and thalamic, attaining a further series of areas by indirect pathways; but the problem lies precisely in the interpretation of the possibility of proprioceptive multiplicity. To visualize this is about as difficult as to imagine the movement of a two-seater bicycle each seat of which is equipped with its own separate set of handle-bars. It is clear that the presence of two effector centres responding to proprioceptive input requires the closest possible co-ordination between them. I would deny neither the possibility that such connections may exist nor that they exist in fact. My aim in the first two sections of this chapter is merely to indicate the great difficulties which confront functional explanations of the co-ordination of movements. It is already apparent that eqn. (3c) is quite different from our usual, qualitatively simple models of the interaction between the centre and the periphery; when, however, we are obliged to confront their complex interaction as a result of the mutual activity of entire systems of organs which, anatomically and clinically, display varying degrees of independence, then the resulting great structural complexity becomes more obvious still. Yet this is fruitful, since a failure to realize the difficulty of a problem frequently defers the moment of its solution.

3. *The Interrelationship between Co-ordination and Localization*

The discussion in the preceding sections has already largely revealed the close connection between problems of co-ordination and localization. It is clear from all that has been said above that no nuance of a single impulse $[E(t)]$ can serve as an explanation of even the simplest case of repeated accomplishment of automatizing movements, and still less as an explanation of the involved complexity of natural movements carried out by many muscles, each

of which involves control from many centres. To digress: at the beginning from the indubitable presence of functional "inter-departmental" connections between brain centres which organize these latter into hierarchical order *(Über- und Unterordnung)*, the following innervational scheme for effector impulses will be obtained (Fig. 17). It is clear that co-ordination is determined not so much by differences in the effect of each of the impulses *Aa, Ab, ...,* *Ba, Bb ...* taken separately, but also by the systematic modes of
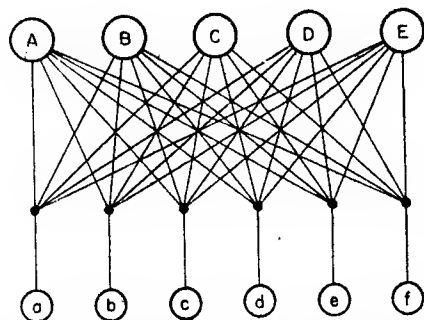

FIG. 17. The multiplicity of efferent pathways for the control of six muscles *a, b, c, d, e, f,* by five effector centres *A, B, C, D, E,* gives, even in this intentionally simplified case, a complex structural scheme of innervation.

their common operation and joint effect. The term co-ordination hints at the common action of separate elements. The solution to the problem of co-ordination lies not in analysis of the tonal and expressive resources of a single instrument in an orchestra but in the technical construction of the score and in the mastery of the conductor.

The basic guiding thesis for investigations of co-ordination must for this reason be formulated in the following way. Co-ordination is an activity which guarantees that a movement shall have the homo-geneity, integration and structural unity which has been described above. This activity is principally based not on particular processes in individual neurons, but on the determinate *organization* of their common activity. This organization must necessarily be reflected in the anatomical plan in the form of localization.

This seems to me to be an extremely expedient way of formulating the question. On the one hand, organization and the forms in which

it exists must inevitably be represented in the structural forms of localization. In the same way as we may derive from an examination of a diagram of an electrical circuit some idea as to the nature of its function, so data of the localization-anatomical type may serve at least as circumstantial evidence in the consideration of the new experimental problems I have put forward—*the structural physiology* of movement. On the other hand, such a structural analysis of movement should aid considerably in critical evaluation of existing movements and future conceptualizations of the type and structure of cerebral localization. It is impossible to visualize a situation in which localizational structure would be found to contradict structural organization.

A pertinent point must be made here. One must not in any way confuse localization with topography. Topography is the geography of the brain, the study of the spatial distribution of its functionally existing points. Localization is the structural plan of anatomical interrelationships between these functional points. If we shuffle in Fig. 17 the positions of the centres *A, B, C, D* and *E,* this will change the entire topographical picture, but will not alter their localizational structure. The distribution (topography) of the elements in a diagram of a receiving set are completely different in the diagram from the topography of these elements in an actual apparatus constructed from this diagram. On the other hand, for one and the same topography completely different schemes are possible.

Figure 18 makes the latter clear in regard to circuit-diagrams which are extremely convenient for illustrating our problems; diagrams (a) and (b) in this figure have exactly the same structure for different topographies, schemes (b) and (c) have the same topography but different structures. The problem which obsessed our physiological forefathers, that of the inversion of the retinal image, and in particular whether this inversion is transmitted in exactly the same way to the cortex, and if so, how it is compensated, appears to us now to be childishly simple-minded. We still remember how some of their contemporaries hypothesized, to explain the matter, that the soul was located in the brain with its feet uppermost, without however determining more precisely whether souls have feet. Nowadays we hypothesize with great facility much more complex transpositions of elements in the representation of the retina on the cortex without experiencing structural difficulties from this fact; indeed, in a central telephone station, for example, we do not

have to worry whether the commutator links for subscribers from the northern and southern parts of a town are located respectively at the northern and southern ends of the switchboard. However, this old question permits of new and less childish formulations; |
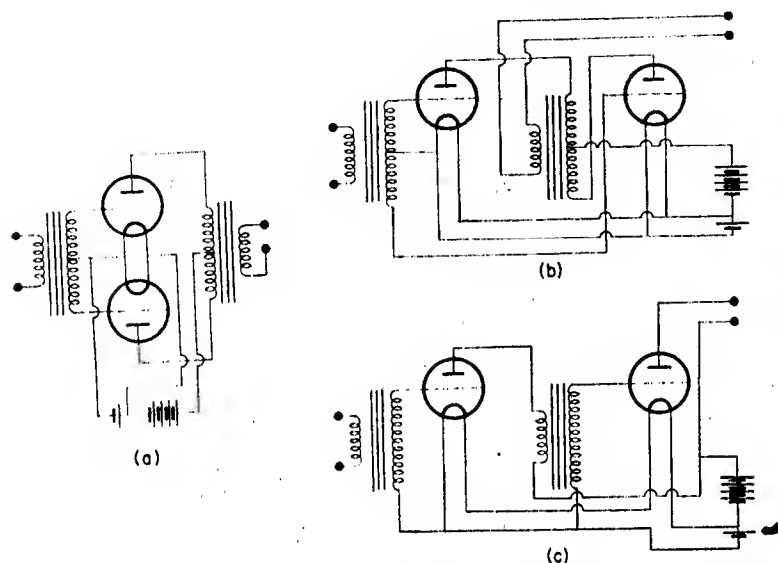

FIG. 18. Three diagrams for two-tube audio-frequency amplifiers. Diagrams (a) and (b) (a single-cascade push–pull block) are identical in all details; that of (c) (a double-cascade amplifier with transformers) is very different in principle from the other systems.

are there, nevertheless, limits to this type of transposition? And if such limits exist, what are the borders which separate transpositions that do not change structure from transpositions which inevitably destroy structure? An analysis of the problem when framed in this way shows us first of all that different structural schemes may show different degrees of tolerance to transpositions, but this aspect of the problem will be developed a little later.

Thus, in the problem of localization what is important for our purpose is not precisely where in the cortex one or another peripheral object or function is reflected, but *what* is represented, and *how*; and what are the distinguishing characteristics of those objects represented in the cortical hemispheres and in subcortical centres.

Topographical problems are for the most part clearly unrelated to the analysis of the co-ordinational structure of movements, while the problems of localization are of paramount and principal significance.

This significance may be very well explained from the example of the old conception of localization which has already been mentioned in Section 1. This conception would answer perfectly to reality if every central impulse unconditionally governed a single determinate movement, that is, if there existed a one-to-one correspondence between impulses and movements. In this case the effector impulses would be able to operate purely as a function of time $E(t)$, giving always one and the same effect independently of what occurred at the periphery; the push-button control-board model of the cortex, similar in plan to an organ keyboard, would be suggested in the types of explanation we employed. But, on the contrary, this type of one-to-one correspondence does not exist and the cerebral motor area organizes responses by deftly adjusting and balancing between resultant external forces and the manifestations of inertia, constantly reacting to proprioceptive signals and simultaneously integrating impulses from separate central subsystems, so that ten successive repetitions of the same movement demand ten successive impulses all different from each other; and the presence in the cortex of localizational equipment of the Hitzig or Foerster type begins to seem a very dubious interpretation. I would like to recall here the failure in 1923 of the invention of "a symphony of whistles". An attempt to convert steam whistles into a musical instrument with an organ keyboard failed because any given whistle could not be relied upon to sound the same on every occasion, and its pitch would vary with the pressure of steam, with the number of whistles sounded simultaneously, with the degree to which the steam-channel was clear, and so on, so that it was impossible to obtain a one-to-one correspondence between the keyboard, on one hand, and the frequencies of the tones obtained, on the other.

It is understood that a statement of complexity, of "impracticality" from our point of view, is not in any sense a decisive argument for the acceptance or rejection of any physiological hypothesis. There is no reason to suppose that physiological structure should be maximally rotational from our technico-social anthropomorphic point of view. The localizational structure of the cortex according to Foerster's scheme (Fig. 16) does not directly contradict eqn. (3c)

with its proprioceptive cycle and lack of simple one-to-one re-
lationships; it only makes the problem of functioning of its cell
centres extremely difficult. The decisive argument against the
theory of direct representation of muscular systems on the cortex
comes from quite another, perhaps unexpected, direction. I present
this argument in its most general formulation below; here I shall
employ only one of its partial modifications as applied to a parti-
cular case.

Let us suppose that the cells of the gyrus centralis are in reality
the effector centre for the muscles. Let us further suppose that the
activity of these cells must be (as is inevitable in the given hypothesis)
sharply different from instant to instant on the multiple repetition
of a given movement, in relation to changes in the external force
field and to proprioceptive signals. If we suppose for clarity that we
may represent each excited effector cell in the cortex as lighting up
like an electric bulb at the moment when its impulse is transmitted
to the periphery, then under such an arrangement the effecting of
every movement will be visible to us on the surface of the cortex as a
zig-zag discharge. The absence of one-to-one correspondence and
all the considerations which have been described above as conse-
quences of eqn. (3c) will be obvious in this case because on every
repetition of a given movement the zig-zag discharge will be
visibly different. Now suppose that this repetitive movement is an
automatized act, the realization of a habit of movement, in other
words, a conditioned motor reflex. From the discussion above it
follows as an inescapable deduction that the conditioned reflex of
movement operates each time through a new zig-zag—through new
cells; in other words, we arrive at the conclusion that the hypothesis
of cellular localization of muscles necessarily leads to a denial of
cellular localization of conditioned reflexes. One of the two chess
pieces must here be taken, and it is here a very pertinent question
which of the two the old-fashioned localizationalist would rather
sacrifice.

I do not for a moment imagine that I can overthrow the old
localizational concept at a single blow, but it is not possible to
disguise the fact that it is already threatened in very serious ways.
The experiments of Bethe [30] and of Trendelenburg on the ex-
tirpation of cortical tissue in monkeys has indicated the pos-
sibility of far reaching compensations and, moreover, the extensive
investigations carried out by Lashley, experimenting on rats and

observing the appearance of compensation and of the re-establish-
ment of conditioned reflexes for the most varied and topograph-
ically different sites of extirpation, are very persuasive evidence in
favour of a radical re-examination of the old conceptions. Lashley
could not discover any clear relationship between the topographical
loci of the areas he destroyed and the degree to which the condi-
tioned reflexes could be re-established; he found, on the contrary,
that there is a strong correlation between the time required for
re-establishment and the quantity of brain substance removed,
without reference to its locus. These results cause him to favour the
theory that there is no cortico-cellular individuality of operation,
in which, it seems to me, he is quite mistaken. His data are extremely
dangerous for the old localizational theory, but they far from
disprove the possibility of any form of localization in general
terms.

Lashley's error sets off very well the opposite error made by Gall
in his time. Nobody now believes that phrenology was doomed to
failure because the very principle of cortical localization was found
to be defective. Nobody ascribes its downfall to the fact that Gall
did not localize avarice or ambition to areas in which they were
located in reality. Gall's theory was essentially faulty not because
of the topography he assigned but because of the principles of
selection underlying those categories for which he thought that he
could find discrete localizations in the cortex. The categories sug-
gested by Fritsch, Hitzig, Foerster, and others appeared to be more
physiological and nearer to reality than Gall's fantasies, which were
impregnated with the moral rationalism of the 18th century, and
appeared, as it were, to be the next approximations to the dis-
covery of reality. The evidence which has accumulated against
these Foersterian categories up to the present time must inevitably
lead to their abandonment, but this does not yet threaten the fall
of the principle of localization in general. It should be recalled that
immediately after the abandonment of phrenology the idea of
localization also appeared for a long while to be compromised until
it gradually became apparent that it was possible that the baby had
been thrown out with the bath water. Now, again, after the develop-
ment and establishment of the understanding of conditioned re-
flexes, to deny the structural anatomically engraved specificity of
the brain would amount to an affirmation that its nature is ab-
solutely beyond knowledge.

Our experimental aim at present lies in the correct formulation of categories which are really represented in the brain centres. The key to this search for the true categories clearly must lie in structural analysis: of the receptor moment, as it appears in experiments with conditioned reflexes; and of the effector moment, as it appears in the co-ordination of movements.

4. *Ecphoria of the Engrams of Movement*

So far I have touched in this report only on those phenomena which point to the momentary, extensively structured nature of the co-ordination of movements. It appeared important to me to demonstrate that a movement could not be understood in terms of some nuance in operation of a single impulse, but that it is the result of the simultaneous co-operative operation of whole systems of impulses, while the structure of this system—its structural schema—is important for the understanding of the result. It is only a short step from this to the central argument in this report, that the innervation and localization of this structure is in reality not only not contradictory to the observable structure of the movements of the organism but is necessarily an exact representation of the latter. To proceed further it is now necessary to attend to another side of the phenomenon, that is, its duration in time. It is necessary to elucidate experimentally whether a simple parallelism exists between the duration in time of a series of system-related impulses or whether there also exists on the co-ordinational time axis the same mutual structural interdependence as has been described above for every separate moment of force.

This formulation of the question may be clarified by the following illustration. In order to achieve a given co-ordination at a given moment, we have Schema I (for example that illustrated in Fig. 18). Is it possible to regard all co-ordinations over all possible durations of time as uninterrupted functionings of Schema I, or do they exist, and may they be regarded as a sequence of changes of Schema I to some other schema, qualitatively different from it (Schema II, and then to Schema III, Schema IV, and so on), while the law of the transition between the schemas and their order of transition, in its turn, has its own determinate structural features? Our factual data on this problem are so far extremely scanty but some observations may still be made.

Firstly, we must turn to the facts described above of the homogeneity of a movement and its unity in terms of the interrelations of its parts in space and in time. Having established our model for a rhythmical movement in the form of a three–four term trigonometric series of the type of eqn. (4), it is possible to prove beyond doubt that this homogeneity also exists in time, and that this particular homogeneity is indeed not peripheral or mechanical but certainly originates in the operation of the central nervous system. This demonstrates that there exist in the central nervous system exact formulae of movement *(Bewegungsformeln)* or their engrams, and that these formulae or engrams contain in some form of brain trace the whole process of the movement in its entire course in time. We may affirm that at the moment when the movement began there was already in existence in the central nervous system a whole collection of engrams which were necessary for the movement to be carried on to its conclusion. The existence of such engrams is proved, however, by the very fact of the existence of habits of movements and of automatized movements.

A problem of considerable structural significance now arises. Let us suppose that to a given co-ordinated movement there correspond, in the brain, n engrams by means of which it is ensured that the movement will take place with successive ecphoria in a determinate time sequence and with determinate tempo and rhythm. All these n engrams exist in the central nervous system at any given moment as the habit of movement exists, but they exist in a hidden, latent form. How are we to explain the facts that, firstly, they do not all undergo ecphoria simultaneously but in sequence, secondly, they do not lose their order of ecphoria, and thirdly, they observe determinate time intervals between ecphoria (tempo) and quantitative relationships in their duration (rhythm)? There are here two basic possibilities, two "temporal structures"; either (a) each successive ecphoria of the engram (or perhaps a proprioceptive signal of its effect at the periphery) serves as an ecphorator for the next engram in order; or (b) the mechanism for ecphoria, the ecphorator, lies outside the engrams themselves and directs their order by a hierarchic principle of *Überordnung*. The first hypothesis may be called the "chain" hypothesis, the second the "comb" hypothesis (Fig. 19).

Very weighty considerations may be found to support both these hypotheses. The chain hypothesis brings to the fore proprioceptive moment, and in this connection it explains independently and satis-

factorily the observation of tempo and rhythm referring them to a regular synchrony with events occurring at the periphery. Because, on this hypothesis, the stimulus for the arousal of each successive ecphoria is the existence of the preceding one, it is possible to explain both the maintenance of an order of succession and the impossibility
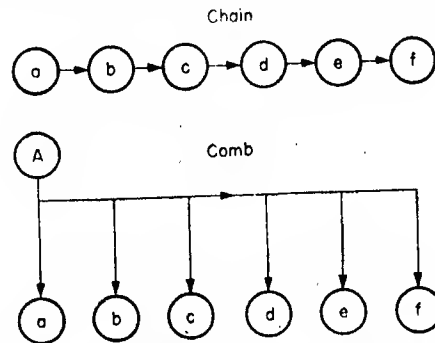

FIG. 19. Two theoretically possible schemes for successive ecphoria of motor engrams *a*, *b*, *c*, *d*, *e* and *f*.

of separate links being left out of a succession of ecphoria in this way. Finally, the hypothesis recommends itself by its simplicity, and by the fact that it is unnecessary to postulate any particular structure for the ecphorator.

The arguments in favour of the comb hypothesis are no less cogent. The presence in the C.N.S. of "the plan of a movement", the homogeneity of its formula and the homogeneity of the movement itself and of its course from beginning to end does not answer to the hypothesis that a movement is fractioned in this way, or that there is no guiding principle of succession among elements of the chain type other than events at the periphery. We do not see in this case any sign of a guiding principle unifying the whole. Further, if we recall the facts discussed above which indicate that the central impulses merely adjust to, and compensate for, the external force field so that the pattern of the impulses over time may have very little in common with the picture of the movement, the comb hypothesis finds a new and important reinforcement. At the same time, a glance at Fig. 14 shows that the central impulse *C*, which is represented by a hatched area (and is entirely unlike the summed rhythmical equilibrium *B* which is finally achieved because of the

presence of external disturbing forces *A*), shows a succession of elements which in no case resemble each other. The possibility of obtaining the homogeneity and regularity of *B* on every repetition, agreeing at the periphery with the law expressed in eqn. (4), necessarily requires the existence in the C.N.S. of some type of guiding engram which encompasses the entire law of succession of *B*. If a guiding engram of this type exists (we may refer to it as the motor image of a movement) it must have a dual nature; it must contain within itself, in some way uniquely and simultaneously existing like an embryo in an egg or a track on a gramophone record, the entire scheme of the movement as it is expanded in time. It must also guarantee the order and the rhythm of the realization of this scheme; that is to say the gramophone record mentioned above must have some sort of motor to turn it. To pursue this metaphor, what I have called the gramophone record is the directing engram, and what I have compared to a gramophone motor is the ecphorator.*

Both of the hypotheses which we have examined are completely bound up with the structure of the peripheral impulse which we have deduced above in terms of eqn. (3c), that is, its dependence on the form $E(t, \alpha, d\alpha/dt)$, but they only illuminate this dependence in different ways. On the chain hypothesis the critical agents which determine the development of the process are the dependence of E on α and $d\alpha/dt$, that is, their proprioceptive relationships, while the temporal moment of the relationship to t is determined in this case only by the tempo and by the maintenance of each individual element of the chain *a*, *b*, *c* (Fig. 19). In the comb hypothesis, on the other hand, the dominant relationship is $E(t)$, that is, the independent initiative and the regulating activity of the C.N.S., and proprioceptive effects merely play the role of correctors to the general whole.

It must not be forgotten that the hypothesis of the necessity for an effector mechanism which is distinct from the engrams

* It is interesting to note here that the question which I have raised of the ecphoria of movements in a chain system or a comb system is a repetition in new terms in the area of the physiology of movement of the ancient psychological dispute of association (Bleuler, Adler) versus action (Berze) in the manner in which psychological processes are carried on. The chain model corresponds to the concept put forward by the associationists and the comb model is very similar to Berze's hypothesis. I am in no sense a partisan of the latter opinion in view of its deeply idealistic basis (the psychology of voluntarism), but I cannot deny that the attacks made on the opinions of pure associationists were extremely opportune.

themselves and is in some sense dominant over them, is not necessarily related to the comb hypothesis but is necessary in equal degree for both hypotheses. Whatever we may ascribe to the regulating engram in the comb hypothesis and to the elementary engrams $a, b, c, \ldots$, in the chain hypothesis they arc all alike bound to contain in latent form the impulse E in dependence not only on α and $d\alpha/dt$ but also on t. It makes no difference whether the central mechanisms of tempo—this "gramophone motor"—is related in its action to the duration of the physico-chemical intercellular reactions or to some other physiological rhythms;* they must in any case exist as some functions which differ from the collection of engrams which they activate, because real time cannot be incorporated in the latter. A decision between alternatives in favour of one or other of these two hypotheses, or perhaps in favour of some other more complex organizational synthesis which incorporates both of them, is a topic for further investigation. At present it is important for us to discover what, in principle, is implied in the actual manner in which the problem is framed.

What is important is that the motor image of a movement (that has been termed by neurologists "the program of a movement", *Bewegungsformel*, *Bewegungsgestalt*, and so forth) must necessarily exist in the C.N.S. in the form of an engram. This directional engram does not merely exist on the comb hypothesis; indeed, the same fact of successive "stamped-in" connections between elementary engrams $a, b, c, d, e, \ldots$, in the chain hypothesis is also the cngram in the other scheme, only in this case it is represented by an arrow rather than by a circle; this is the engram that determines the law of systematic succession of ecphoria and that consequently controls it. This motor image corresponds to the real, factual form of the movement, that is, *to the curve B* in Fig. 14, and in no way to the curve of the impulse C; it is indeed true that its presence makes it possible to control the course of the impulse C so that, as a result, a smooth performance of the movement habit B is achieved. Therefore it is necessary that there should exist in the supreme nervous organ an exact representation of what will later occur at the periphery; meanwhile, the unfolding of the activity in the field in the intervening operational stages and the

* For example, the velocity of the dispersion of waves of excitation through the C.N.S., time phenomena related to the interference of these waves, rhythmical heart activity, etc.

realization of the impulse C (which by the argument given above is accordingly dissimilar to the peripheral effect), must therefore also be dissimilar to the contents of the controlling engrams. We may use the following metaphor: it is as if an order sent by the higher centre is coded before its transmission to the periphery so that it is completely unrecognizable and is there again automatically deciphered. In Section 3 above I have said that the possibility of a habit of movement, of the establishment of a conditioned motor reflex, necessarily implies its unitary localization in the central reflex, necessarily implies its unitary localization in the central areas, and that a unity of this type cannot be related to the theory of the representations of muscles in the higher centres of the cortex. The considerations which have just been raised once again confirm this thesis, on this occasion from the point of view of the time structure of movements; that level of the C.N.S. in which the centrifugal impulse C is formulated and in which we might consequently expect to find a representation of the muscular system is not the supreme level of the C.N.S., but is in fact that level at which the elementary engrams $a, b, c, \ldots$, etc., of the comb hypothesis are located. Between the mechanism represented by the comb hypothesis and the mechanism involved in the case of muscular rethesis and the mechanism involved in the case of muscular representation we are obliged to insert another process of the coding of the image of the movement and its presentation in the form C. In the terms of our equation this coding process is the transformation of the relationship $E(t)$ in the pure form prevalent in the higher level into a full dependence of the form $E(t, \alpha, d\alpha/dt)$; that is, the adaptation of the impulse to proprioception.*

* The formation and development of new habits of movement, that is, the engraphy of conditioned reflexes of movement, also appears to be a structurally complex process in the light of the analysis undertaken in this report. It is in fact the case that new directional engrams with their spatio-temporal details must be built up in the C.N.S.; however, those auxiliary proprioceptive mechanisms which I have just described as "coding" the impulse, and which provide the higher engram with the possibility of an actual detailed existence, must also be built up. The fact that the habit of movement is not engraphed in those centres in which the muscles are localizationally represented is at once demonstrated by the fact that an acquired habit may exist while incorporating very different muscles in various combinations. When a child learns to write he can only form large letters, but a literate adult can form either large or small letters with equal facility and write either straight ahead or sideways, etc. Apparently the motor directional engrams are developed, generally speaking, later than the auxiliary coding mechanisms and correspond to a higher degree of mastery in the acquisition of a habit.

In this way, the analysis of the course of a movement in time again brings us to a recognition of the structural complexity of an act of movement, and consequently also of the complexity of its representation in terms of localization. Here, also, the recognition of the necessity for the existence of directional engrams and mechanisms of ecphoria demands that we postulate a series of hierarchical levels, each of them, inevitably, having a degree of qualitative independence.

5. Topology and Metrics of Movements. The Motor Field*

If we now turn from the temporal moment to the spatial it will be necessary to touch on two considerations: the distinction between the metric and topological properties of physiological space, and the peculiarities of the motor field of the central nervous system. Because of their fundamental importance these two points should really be the objects of separate reports. I will for this reason discuss them only as much as is necessary to develop my basic thesis.

In any geometrical representation we may make a distinction between topology and metrics. By the topology of a geometrical object I mean the totality of its qualitative peculiarities without reference to its magnitude, form, any distortion in its reproduction, etc. As topological properties of a linear figure, for example, we may discuss whether it is open or closed, whether the lines composing it intersect with each other as in a figure eight or whether they do not intersect as in the case of a circle and so on. Besides these properties, in the determination of which quantitative considerations are irrelevant, we may also consider such topological properties as incorporate the concept of number, not, however, including the concept of measure. Among these properties we may refer, for example, to that of quadrangularity, membership in the group of five-pointed stars, and so on. I shall arbitrarily describe this group of properties as topological properties of the first order while the former may be

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* The term "topology" as used here does not coincide exactly with the strict mathematical definition. For lack of a more adequate expression I have adopted this term for the whole of the *qualitative* characteristics of space configurations and of the form of movements in contrast to the quantitative, metric ones. The more detailed definition of what is meant here under the term topology will be understood from the text.

considered zero order properties. All figures in the upper row in Fig. 20 belong to one and the same topological class of figures of the first order (being, however, completely dissimilar in metric relations); they are indeed identical in respect to the numbers which characterize them. All of them have five angles or points, all of them display five intersections of the lines composing them, and so on. No. 6 in this illustration belongs to another class of the same order
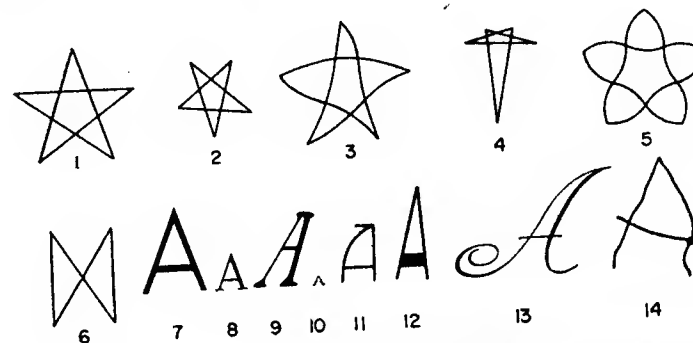
FIG. 20. 1–5, topological class of five-pointed stars; 6, topological class of figure-eights with four angles; 7–14, topological class of letters *A*.

containing four angles and one intersection, but it is located, as are the first five figures, in the class of zero order, being as they are a closed figure with intersecting lines. In order to illustrate characteristic properties of the first order with an example with which we are all familiar I shall point out that every printed letter is a separate topological class of the first order, while to the single class of letter *A* there belong letter *A*'s of all dimensions, scripts, outlines, embellishments, etc. (see 7–14 in Fig. 20), though we ignore certain additional details of purely calligraphic significance. The chalk figures for the game of "hopscotch", which appear in great numbers on our pavements every spring, are also all representatives of one and the same topological class of the first order for each equivalent and the same topological class of the game, and in this respect the scale of the figure representation of the game, and in this respect the scale of the figure or the age and skill of the draughtsman do not matter. The habitual scheme on which a given child draws a house or a face is also usually a determinate topological class and nothing more.

After this general introduction we may turn from geometry to

psychophysiology. If we draw the attention of a psychologist or a teacher to our collection of letter A's in Fig. 20, he will immediately remark that the whole set displays a common characteristic in terms of its essential sign, that is to say without circumlocution, that the topological characteristics of a figure are of paramount psycho-logico-pedagogical importance in comparison with properties of a metrical sort. Our psychologist or teacher will be quite right, because the recognition of the letter A does not require the presence of any metrical properties and is, on the contrary, entirely dependent on the presence of determinate topological cues. This great affinity between the process of recognition and topology, which has also been noted and studied for some considerable time by adherents of Gestalt psychology, is certainly a psychophysiological phenomenon and may even be of general biological significance, but in any case it cannot be deduced from purely geometrical considerations. The biological characteristic of the predominance of topological categories over metric ones may be pursued in a multiplicity of examples. A maple leaf differs from a birch leaf in respect to topological properties of the first order, while at the same time all maple leaves belong to one and the same topological class in spite of all the thoroughly investigated biometric variation between separate specimens. The structure of the brain and the disposition of the main convolutions of the cortex again provide an example of an object having the same topology for all possible metrical variations. It is possible to say with certainty that in the area of biological morphology those cases in which metrics is of importance together with topology (for example, the lens of the eye) are rare exceptions.* This overwhelming importance of topology in the case of living objects should be attentively compared, for example, with the morphology of crystals where the essential relationships are all metric ones.

A whole series of biologically important morphological signs must unquestionably be referred to topology, although they cannot be numbered either in the zero or in the first order. Every child will naturally distinguish between a cat and a dog; the distinction is certainly not made on the basis of anatomical considerations such as the comparative structure of the claws and the teeth, on which

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* It may never cross the mind of an anatomist or a topographical anatomist that all his life he considers only various topological categories—a new variation of Molière's M. Jourdain!

topic he may be fully ignorant, but on the general appearance—on a certain *je ne sais quoi*—that indubitably appears to be a topological category. However, the difference between the appearance of a cat and a dog cannot be related to topological signs of the first order. It is likely that some higher orders which await future analysis are operating here.

Insufficient attention has so far been given to the fact that the movements of live organisms, to no less a degree than their perceptions, are determined by topological categories. This is illustrated with great clarity by the example of drawing, perhaps because this type of movement leaves a record which may be conveniently studied. It is easy for everyone to draw a five-pointed star, but we can say with certainty that this picture is made by using only topological and not metric relationships. As proof of this I suggest the experiment of drawing ten such stars in succession and comparing the pictures. I doubt if it is at all possible to make a metrically perfect copy of a similar object without the help of a compass and a ruler, that is, the human motor system cannot attain any high degree of metric proficiency, but it can be said that our motor system is very sensitive to topological distinctions of higher orders than one and zero. It is sufficient, for example, to draw attention to hand-writing. I pointed out above that the letter A belongs to a single topological class of the first order no matter how or by whom it is written. Besides this, all letter A's written in my hand are similar to each other and are simultaneously different from letter A's written by second and third persons. The similarity between my A's is far from metrical, but is topological; the differences between my A's and those written by other hands must in the same way be related to topological differences involving higher orders than the first. The topological propensities in our perception seize upon what may be regarded as common features within the limits of a given handwriting—once again in a form which it is not easy to subject to analysis in terms of impressions—a *je ne sais quoi*, the analysis of which is not yet practicable for us because of our lack of acquaintance at present with whatever may constitute higher topological orders and what properties we must ascribe to them.

Such of our movements as do not leave a trace upon paper have drawn less attention to themselves in the manner indicated. Parallel with the knowledge on handwriting there exist structurally similar bodies of knowledge on gait, touch in music and accent of voice,

although the analysis of these phenomena has not been carried very far. One thing may, however, be already affirmed with certainty; all attempts to draw distinctions of this type in terms of quantitative metrical signs (as can be done, for example, with pitch) are doomed to failure in advance. It is here necessary to make new discoveries in qualitative geometry, but consideration of the perspectives which are now unfolding in this direction would be for us at present too far from our main goal.

A circumstance of great and immediate interest in the structural analysis of movements is the fact that topological peculiarities in visual perception display marked similarities to some signs of idiosyncrasies in the topology of motor organization. So, for example, the category of dimension is equally indifferent to visual perception and to movement. I find it equally easy to recognize a triangle, a star or a letter whether it is presented to me in a large or in a small form. The same indifference to the absolute dimensions of a geometrical object was demonstrated in dogs by Pavlov and in rats by Lashley. In precisely the same way I find it equally easy to draw a star or write a word large or small, and to do this on a piece of paper or on a classroom blackboard. It would be interesting to make a study of the quantitative relationship between the variation in these drawings and their size; but we may say in any case that, whatever the size, they retain their topological properties not only of the first but also of higher orders; so, for example, all the characteristics of handwriting which are peculiar to a given person when writing on paper are also apparent in writing on a blackboard, although, in a word, the entire muscular structure of the movement is absolutely different in the two cases.

Visual perception, however, shows great sensitivity to such concomitantly metric cues as symmetry, a category that is at the same time completely ignored by the motor system. On the other hand, the metrical category of extensity is, without doubt, of greater importance to the motor than to the visual receptors because the estimation of dimension in perception (for example, visually) is always ultimately based on deep-seated kinaesthetic associations related to the field of sensitivity of the receptor. The perceptual and motor systems are to all appearances equally indifferent to the category of position in space (right, left, above, below), which is of exceptional interest for the structural analysis of localization. In fact a figure which may be placed in the most diverse portions of the visual field

is recognized with equal facility as being the same;* in the same way the process of carrying out an habitual action, for example, writing a word or playing over a passage which one has learnt by heart on the piano, is carried out with approximately the same facility and with the same degree of accuracy independently of the position of the hand or of the register on the piano. It is interesting that the purely metrical abilities of the kinaesthetic apparatus (for example the estimation of length or of distance) are characterized by gross differences in various zones of the spatial field.

Both perceptual recognition and motor reproduction are extremely sensitive to the orientation of a figure in space. The identification of a triangle after it has been rotated 180° is incomparably more difficult than the identification of triangles of different size with the same orientation. In just the same way it is extremely difficult to draw figures upside down with a pencil.

It is an important fact that in a very large percentage of cases children draw the mirror images of letters, that is to say they change about the right and left sides although they never turn the letter upside down. Another fact is also interesting (being indicative of some sort of structural hierarchy); children never either read or write an entire word from right to left, they only do this separately and successively for individual letters of the word. It is clear that in both these cases there must exist different mechanisms which cannot be compared to each other.

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* I consider this fact to be an extremely clear illustration of the structural complexity of every conditioned reflex, even what is apparently the most simple one. In presenting a conditioning stimulus visually to a dog neither the head, and still less the eyeballs, are in any way immobilized and for this reason the visual stimulus may fall on the most various points of the retina, and consequently on different points of the first visual centre. If the visual stimulus is, for example, a triangle, on each presentation of this stimulus to the animal's retina a whole series of sensory elements are excited, and here, every time the animal turns its head and eyes this series is either wholly or partially different. The appearance of a single reaction in all these cases proves, it would seem, that the engram for a given conditioned reflex is not located at those points (the primary visual centre) on which the separate lines and points are represented but at some structurally higher centre, the connection of which to the former is very similar to that which has earlier been described in the case of the successive levels of the centres of movement. Here we find an example of the same fact which was employed above (section 3, p. 29) as proof of the impossibility of localization of the muscles and of conditioned reflexes in one and the same centre.

These analogies and differences may be pursued to great lengths: a study of these and others promises to be extremely fruitful. At present, however, it is necessary only to summarize all that has been said above about the topological properties of perception and movements.

First of all, it may be stated that the totality of the topological and metrical characteristics of the relations between movements and external space can be generalized under the term *motor field*, analogous with the concept of the visual field recognized by psychologists. An immediate task of physiology is to analyse the properties of this motor field. The preceding statements permit us to assert that the physiological motor field is as widely different from objective external space as is the visual field. Its typical differences from theoretical Euclidian space consist, first of all, in an obvious preference of the motor field for topological categories as compared with metric ones, in the presence of some evident tropisms, or tendencies toward certain directions, in the absence of bilateral symmetry (which is peculiar to the visual field), and so on. The predominance of topology is revealed also in the fact that straight lines and their distinction from curved ones are not proper to the motor field (in this it differs from the visual), nor are stable, identical lines. In biomechanics this is manifested in that successive movements of cyclical nature never exactly repeat themselves (Fig. 21). The co-ordinational net of the motor field must be regarded, in distinction to a net in Euclidian geometry, firstly as non-rectilinear, and secondly as oscillating like a cobweb in the wind. Its "oscil-
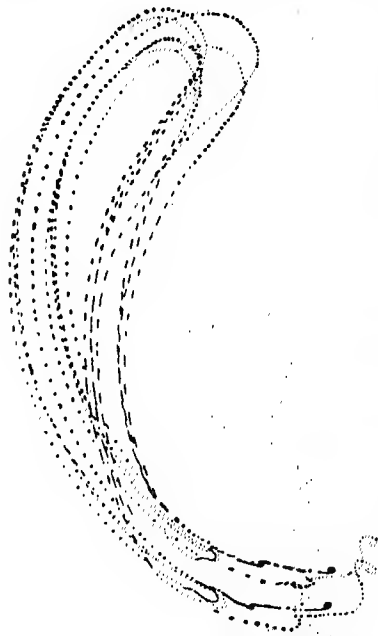
Fig. 21. Cyclogram of a series of successive poorly automatized movements taken on the same plate.

lation" does not, however, in every case proceed so far as to destroy topological relationships either of zero order (for example the category "between") or of the first and perhaps of even higher orders.

Some of the properties of the motor field which we have now disentangled are of great interest for the theory of localization. Firstly, there is the deeply seated inherent indifference of the motor control centre to the scale and position of the movement effected, as we have discussed above. It is clear that each of the variations of a movement (for example, drawing a circle large or small, directly in front of oneself or to one side, on a horizontal piece of paper or on a vertical blackboard, etc.) demands a quite different muscular formula; and even more than this, involves a completely different set of muscles in the action. The almost equal facility and accuracy with which all these variations can be performed is evidence for the fact that they are ultimately determined by one and the same higher directional engram in relation to which dimensions and position play a secondary role. These engrams, which determine the muscle structure of each of the concrete variations, clearly lie still lower than those described in section 4 and in particular in the area C of Fig. 14, whereas the engrams of dimension and spatial position may already be referred to area B. We must conclude from this that the higher engram, which may be called the engram of a given topological class, is already structurally extremely far removed (and because of this also probably localizationally very distant) from any resemblance whatever to the joint-muscle schemata; it is extremely geometrical, representing a very abstract motor image of space. This makes us suppose—for the time being merely as an hypothesis though it forces itself upon us very strongly—that the localizational areas of these higher-order motor engrams have also the same topological regulation as is found in external space or in the motor field (and that in any case the pattern is by no means that which maintains in the joint-muscle apparatus). In other words there is considerable reason to suppose that in the higher motor centres of the brain (it is very probable that these are in the cortical hemispheres) the localizational pattern is none other than some form of projection of external space in the form present for the subject in the motor field. This projection, from all that has been said above, must be congruent with external space, but only topologically and in no sense metrically. All danger of considering the

possibility of compensation for the inversion of projection at the retina (section 3) and many other possibilities of the same sort are completely avoided by these considerations. It seems to me that although it is not now possible to specify the ways in which such a topological representation of space in the central nervous system may be achieved, this is only a question of time for physiology. It is only necessary to reiterate that the topological properties of the projection of space in the C.N.S. may prove to be very strange and unexpected; we must not expect to find in the cortex some sort of photograph of space, even an extremely deformed one. Still, the hypothesis that there exist in the higher levels of the C.N.S. projections of space, and not projections of joints and muscles, seems to me to be at present more probable than any other.

6. The Principle of "Equal Simplicity"

It is now time to give a general formulation of an heuristic principle which I have already presented in a partial modification in section 3 above, and to examine its application in terms of a few examples. I shall call it the *principle of equal simplicity*.

I begin with non-physiological examples. I have three devices with which it is possible to draw a circle; a circular template, a compass and an ellipsograph. A circle of the same radius as the template may be drawn as easily with the template as with the compass; a circle may also be drawn with the ellipsograph, as it is a particular case of an ellipse, but it will be a little more complicated to do this than with either the template or the compass. If we have a circle of some other radius the template immediately becomes useless. The compass draws circles of all radii with equal facility. A given actual ellipsograph may only describe a circle of a single determinate radius, and for this reason it is eliminated together with the template. If we wish to draw an ellipse we may do this using the ellipsograph with exactly the same difficulty, no more or less than we had in drawing the circle, but both the compass and the template are useless.

In this example we are considering a set of curves of the second order which differ (a) in radius and (b) in eccentricity. One of our instruments, the template, gives us with great simplicity one curve

and no others. The second instrument gives us equally easily all variations in radius, but only a single eccentricity, zero, peculiar to a circle. The third instrument gives us with equal ease—although in absolute terms the process is slightly more complicated than in the case of the compass—all eccentricities, but only one radius. A circle of the same radius as the template may be drawn by means of all three instruments but the functional relationship between their simplicity and the possible variations in all three cases are quite different. The type of this functional relationship is determined with great accuracy by the scheme of construction of the instrument.

In mathematical language the preceding example may be presented in the following way. We designate the degree of simplicity (for example the speed with which the task can be completed, or unity divided by the time of completion, etc.) by S, the radius of the circle by r and the eccentricity by e. Then, for all our devices,

$$S = F(r, e). \tag{6}$$

For the template of radius r we have:

$$F(r, e) = 0; \qquad F(R, O) \neq 0. \tag{6a}$$

For the compass:

$$F(r, e)_{e \neq 0} = 0; \qquad F(r, 0) = \text{const} \not\equiv 0. \tag{6b}$$

For the ellipsograph:

$$F(r, e)_r \neq_R \qquad F(R, e) = \text{const} \neq 0. \tag{6c}$$

Equations (6b) and (6c) may be represented by a line; eqn. (6a) is the point of intersection of the lines (6b) and (6c).

Examples are possible in which the degree of simplicity does not change abruptly from zero to some final value as in the preceding case, but changes from one value to another with a certain regular continuity. So, for example, in multiplying numbers with Odner's calculating machine the degree of simplicity (or the speed of the work) decreases in parallel with an increase in the number of multiplication signs and with the number of units involved with each of

these signs. At the same time the degree of simplicity is invariable with respect to the number of digits multiplied. In the Millioner machine the degree of simplicity is invariable in respect calculating machine the degree of simplicity is invariable in respect to the number of digits in the multipliers and depends only on the number of multiplication signs. Finally, on a slide rule the degree of simplicity is almost invariable with respect to both components involved.

In all these cases we encounter the same fact, that different structural schemes may carry out the same set of operations but the differences in their structures are always accompanied by differences *in the form of the function S*. We may say with certainty that the more marked are the changes in S in the transition from one element of the set to another adjacent to it, the smaller is the degree of the adaptation to this transition possible with the structural peculiarities of the system in question. On the other hand, for any given system there are "lines of equal simplicity", that is, those transitions from one element of the set of possible tasks to another which do not result in any change in the simplicity of manipulation, corresponding to transitions which are most closely related to the structural scheme of the device.

We arrive from this case to the following formulation of the principle of equal simplicity: for every system which is capable of undertaking a set of different elementary processes of a given range, the lines of equal simplicity correspond to those directions in this range along which movement does not involve any change either in the structural principles or in the principles of operation of the system. Instead of the expression "simplicity" which does not have any concrete association we may insert a whole series of parallel expressions in relation to the case under investigation: the expressions of speed of completion, degree of accuracy, degree of variance and so on. For a general formulation I have selected the term simplicity as being the most general in spite of its lack of concrete associations.

We may extract an heuristically valuable principle from the discussion above. If we are concerned with any given system, the structure of which is unknown to us but whose operation we may observe under a variety of conditions, then by a comparison of the changes *in the variable S* (speed, accuracy, variation, etc.) encountered as a function of each of the variables in the conditions, we may come to determinate conclusions as to

the structure of the system which are unattainable by direct means.

Let us imagine, for example, that we are invited to see a film without having any idea of how cinematography works. We may suppose that we are attending it in a puppet theatre (as our grandfathers might have). We are astonished by the wealth and variety of the material we are shown, exceeding by far all that could be met with in these days, but we still have an indisputable right to consider that we are watching only marionettes which have been greatly improved in principle. It is true that in a puppet theatre we never, for example, saw the sea; but then (says grandfather) it is obvious that here they have only an extremely cunning mechanical imitation of the sea. In the old puppet theatre figures could not be made to diminish as they grew more distant, as this occurs in the cinema, but once again it is possible to consider this as a new achievement of the technology of the marionette theatre. All this, although extremely difficult, is possible. It is, however, very easy to show that we are not in a puppet theatre and to do this precisely with the help of the principle of equal simplicity. It is sufficient, for this purpose, to select two objects which are sharply different in their difficulty of representation in the puppet theatre, for example, a rotating wheel and a stormy sea, and without reference to cinematic technique (let us suppose that its technical structure is inaccessible to us) to turn to the studio's accountant and ask how much it would cost to obtain representations of both these objects on the screen for one minute. As soon as we discover that a strip of 20 m of film costs about the same for either object (or, to put it more accurately, that the cost of the film is related to some other arbitrary factors and in no way to the mechanical properties of the objects on the screen), the hypothesis of a puppet theatre collapses. In general, a skilful interview with an accountant may give many positive technical details—we may recall that it was in just this way that Mendeleev discovered the secret of an important French explosive.

For the puppet theatre all is possible (at least potentially) that is possible to the cinema. But the "all" is, in principle, unattainable with the same degree of simplicity as operates in the cinema. We encounter the same interrelationships between the gramophone and such talking machines as were experimented with a hundred years ago by von Kempelin, for example. The whole structural nature of the gramophone lies in the fact that the sounds to be reproduced make

no difference to it, whereas von Kempelin would have been obliged to construct a new mechanical gullet for each new pitch. A rural deacon in L. Andreev's story was brought into an extremely amusing collision with the principle of equal simplicity as applied to the gramophone when he could not conceive how the gramophone could reproduce with equal ease both a music-hall song and the voice of the Son of Man. The principle described proves to be extremely fruitful in its application to the structural analysis of the function of the central nervous system, both in its receptor and in its effector aspects. In section 2 I used a circular movement of the extended arm of the type shown in Fig. 15 as an example of the smooth redistribution of muscle pull. We may return to consideration of the same tion of muscle pull. We may return to consideration of the same movement from a new point of view. If a circle is described with the arm directly to the front, then directly out to one side and then about some intermediate axis, both the muscle and the innervational schemes of the three movements will be sharply different. However, all three movements are subjectively very much alike in terms of difficulty and objectively they display approximately the same amount of accuracy and of variation. This allows us to conclude with a high degree of probability that the structure of the central complex which governs the production of a given series of movements is much more closely related to spatial form than to muscle scheme, because all three variations of the circular movement which we have attempted lie on lines of equal simplicity in regard to the properties of the movement and the properties of their forms, but not the properties of the muscular schemes. This conclusion may be made more clear from the following example, which I have thoroughly analysed in another study [23]. In order to carry out with precision any given automatized movement, for example, cursive writing, the positions and the means of fixation in the intermediate links of the arm are almost completely indifferent. I write with the same handwriting and with almost equal ease when I rest my forearm on a table-top and when my arm supports its own weight, as well as in a variety of positions. All these variants are sharply different from the point of view of muscle structure and if it were assumed that the object of the working out of a habit of movement were one of these structures we would be obliged to suppose that the others would lie completely outside the range of this habit, that is to say, on a quite different level of simplicity. The fact of identical simplicity and the retention of the characteristics of the

habit is immediate evidence that the habit of writing is not a habit of the muscle scheme and consequently that the traces in the C.N.S. which govern these habits are closely related to the topology of handwriting and considerably removed from joints and muscles. All these, and many similar examples, must be experimentally analysed both qualitatively and quantitatively and each such analysis allows us to arrive at new basic conclusions as to the structure of the activity of the motor centres of the C.N.S.

An extremely interesting example of the application of the principle of equal simplicity may be taken from the psychology of perception which is, at the moment, far more developed than the structural physiology of movement. This example refers to a theory of hearing. A whole series of hypotheses have been put forward in order to explain the mechanism operating in the inner ear and allowing us to discriminate sounds (Helmholtz, Ewald, Hering, Gray) among which the most popular at the moment is Helmholtz's hypothesis. On this hypothesis each of the numerous fibres of the basilar membrane is supposed to act as elastic string tuned to a particular frequency. When this particular frequency operates on the organ of Corti and the basilar membrane the given fibre goes into a condition of resonant oscillation and mechanically stimulates the auditory receptors attached to it. In this way each of the sensitive endings of the acoustic nerve are stimulated only by a single sound frequency and the recognition of the frequency in the C.N.S. is achieved by the same process which effects the perception of tactile local signs *(Lokalzeichen)*. Complex sounds or harmonics are analysed in this way which explains the recognition of pitch and the discrimination of chords.

Many serious psychological objections have been raised against this hypothesis. Additions and corrections were soon made. Helmholtz himself was not able to explain in these terms the perception of consonance and dissonance for which he was obliged to hypothesize the presence of a separate system perceiving beat *(Schwebungen)*. There have been numerous later additions and emendations (F. Alt, A. Gray, L. Hermann Waetzmann, Budd-Feldafing, W. Köhler, G. Revesz, F. Brentano, and others), and the very fact of their necessity has cast serious doubt on Helmholtz's hypothesis. It is very probable that should a new hypothesis appear which adequately explains all the requisite phenomena and is at the same time simpler, it would be preferred to the older hypothesis on the

principle that the true explanation is the simpler one* (although there is nothing objective in this guarantee). However, no hypothesis of this type has so far appeared. Meanwhile, there are serious objections to Helmholtz's hypothesis independent of its simplicity or complexity. It is only necessary for this purpose to show (and there are in the literature an enormous number of experimental and clinical facts pointing in this direction) that the lines of equal simplicity are distributed in an essentially different way for the function of auditory perception and for a resonant harp. So as not to encumber this report I shall limit myself to two points.

We are making a comparison between a system whose functional operation is unknown to us, the apparatus of auditory perception and a known physical model—a set of resonators which for the sake of vividness I have called a resonant harp. For this latter structure the simplest of all operations is the determination of the absolute frequency of a tone; this follows from its very structure. The determination of the relationship between the frequencies of two tones with its help is already a secondary operation, which is only possible after the determination of the absolute frequencies of the components, and is for this reason more complicated. However, the statistics of musical pedagogy (J. v. Kries, O. Abraham, G. Revesz) show that the possession of absolute pitch is a very rare occurrence while a majority of people have relative pitch. In other words, for the organ of hearing relative determinations of intervals are easier than those of absolute tones.

On the other hand, a pure musical tone is simpler in its acoustic structure than the sounds of the human voice—vowels with their numerous formants, and consonants with their characteristic phonation. For a resonating harp these can be recognized in no other way than by their analysis into simple components and only after the determination of these components; consequently, on this model the discrimination of speech sounds is more complicated than the discrimination of pure tones and is based entirely on the latter

* This conviction may very easily be false. Contemporary physics provides various examples of this. The theories of de Broglie, Einstein, Heisenberg, Schrödinger or Dirac are far more complicated than the concepts which they have supplanted. To set up simplicity as a criterion of reliability would be to affirm in principle that the categories of logic and psychology dominate the categories of objective reality and determine them, and we have no authority for apriorities of this type.

process. As far as the human organ of hearing is concerned, *many* people have musical (relative) discrimination while *all* understand and perceive speech. Very striking cases of tone deafness have been described (L. Alt, W. Köhler). Köhler's patient not only did not understand what was meant by a melody, but was even unable to understand what was meant by a melody, but was even unable to distinguish between a low and a high tone, while he could distinguish all shades of speech and accent very well, indeed, imitating provincial accents quite well in telling anecdotes (such persons have no physical defects of hearing). We again find an inversion of the levels of difficulty with respect to the resonator apparatus which we have hypothesized.

It is clear from both comparisons that the organ of hearing gives an essentially different gradation of simplicity than that of the hypothesized resonator mechanism—a gradation amounting in some examples to a direct transposition of the order of difficulty. It is this circumstance which is critically dangerous for Helmholtz's hypothesis, independently of its simplicity or complexity.

The discussion in section 3 of the example of the lack of correspondence between the theory of muscle localization in the cortex and the idea of the localization of conditioned reflexes is clearly a particular case of the use of the principle which has here been described in full. Further experiments and observations on changes in the accuracy of movements in their different variations and for corresponding changes in the irradiation of a habit of movement may disclose for us a whole series of structural regularities in the motor field, and the motor functions of the brain in their entirety—regularities which cannot be foreseen at present. Only one thing may already be foreseen with certainty. Every new discovery in the field of co-ordinational structure will at the same time be a new discovery along the lines of localizational structure; and on that day when we understand the one we shall be able to say that we understand the other.

Symbols Used in this Chapter

I. SPATIAL COORDINATES

x longitudinal (sagittal) coordinate.
y vertical coordinate.
z transversal coordinate.

For x, positive direction is forward.
For y, positive direction is upward.
For z, positive direction is to the left.

II. Symbols for Parts of the Body

Initial letter	Limb		Centre of gravity of the limb segment	Proximal joint of limb segment
	Latin term	English term		
c	caput	Head	gc	—
b	brachium	Upper arm	gb	b shoulder joint
a	antebrachium	Fore arm	ga	a elbow joint
m	manus	Hand	gm	m wrist joint
t	truncus	Trunk	gt	—
f	femur	Thigh	gf	f hip joint
s	sura	Shin	gs	s knee joint
p	pes	Foot	gp	p ankle joint
H	homo	The whole body	gH	—

III. Terms for the Centres of Gravity of Systems (Examples)

The centre of gravity for the system (shin + foot) $g(sp)$.
The centre of gravity for the system (whole leg) $g(fsp)$, etc.

Other points along the long axes of the limbs are indicated by Greek letters corresponding to the initial letters of the Latin term for the limb. For example:

φ a point on the longitudinal axis of the thigh (f).
π a point at the end of the foot (p).

IV. Symbols for the Mechanical Functions of Movement

S displacement (along a line described by real coordinates).
V velocity.
W acceleration.
F force.
M moment of force.

The symbols for joints or centres of gravity of a limb segment are attached to these letters as subscripts. Symbols for coordinates are given in parentheses. For example:

$S_a(y)$ the vertical component of the path followed by the elbow joint.
$V_s(x)$ the sagittal component of the velocity of the knee joint.
$W_\pi(z)$ the transversal component of the acceleration of the end of the foot.
$F_{gs}(y)$ the vertical component of the force at the centre of gravity of the shin.
$F_g(fsp)(x)$ the longitudinal component of force at the centre of gravity of the whole leg system.
M_f the moment of force at the hip joint.

Addenda

1. A point on the facial plane of the head in the region of the upper edge of the aural helix is projected upon the centre of gravity of the head in profile photographs, and is provisionally termed the semi-centre of gravity on these photographs, and is designated by $gc/2$.

2. The angles mentioned in this handbook are designated as follows:

α the angle of the longitudinal axis of the thigh to the horizontal, directed forwards.
β the angle of the longitudinal axis of the shin to the horizontal, directed forwards.
ϕ the angle between the longitudinal axes of the thigh and shin.

CHAPTER III

BIODYNAMICS OF LOCOMOTION

(Published in *Studies of the Biodynamics of Walking, Running and Jumping*
by the author and co-workers. Researches of the Centr. Scientific Inst.
of Physical Culture, Moscow 1940)

1. *Source Material, Points of Departure, Techniques*

On beginning the cyclogrametric investigation of locomotion in 1926, we set ourselves a very restricted and practical aim: the investigation of force phenomena at the centre of gravity of the whole body in walking and running in order to deduce dynamic coefficients for use in the design of footbridges.*

In subsequent years we came to the conclusion that locomotion could also provide very extensive and interesting material for investigations from the physiological point of view.

The advantages of locomotion considered as an object for investigation of the processes of movement are essentially as follows.

Firstly, locomotor movements, in particular walking, are amongst the most highly automatized of movements. The most rigid succession of all details is followed from cycle to cycle and these details are extremely repetitive for each particular subject. This allows one to fix one's attention and to adopt constant criteria for the discrimination of the random from the regular.

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* The principal result of this research was the finding that the amplitude of vertical dynamic forces at the centre of gravity of the body in walking, in other words, the amplitude of vertical reactions of the supporting surface is proportional to the square of the step frequency: $A = \pm P \cdot Q n^2$, where P is the static weight, n the number of single steps per sec, $Q = 0.095 \pm 0.005$ for normal gait. In the case of carrying a load (up to 120 kg) on the back the value of Q rises to 0·100–0·110. Running is characterized by the inequality $A > P$; in fast running the maximal values of vertical dynamic force can reach more than $3P$. The longitudinal components of force in walking and running depend on the length of the step, and we could not find simple expressions for them.

Secondly, locomotor movements display an extremely widespread synergy incorporating the whole musculature and the entire moving skeleton and bringing into play a large number of areas and conduction pathways of the central nervous system. We may therefore expect in them the most clear-cut reflection of the interaction of central and peripheral processes, with a great abundance of detail characteristics of the process of movement in general.

Thirdly, locomotor movements have generality. Their selection as an object of investigation assures the investigator of a large number of subjects who have all mastered, for example, the art of walking incomparably better and more completely than any of their individual professional skills. The beginning and the development of locomotion in normal subjects is achieved with no less regularity and orderliness than is found in morphological development and the development of tissues and organs. This generality and regularity guarantees material for broad comparisons and opens the way to a study of the ontogeny of movements, their growth, establishment, development and involutional disintegration.

Fourthly, locomotor acts belong to the category of extremely ancient movements. They are phylogenetically older than the cortical hemispheres and have undoubtedly affected the development of the central nervous system in the same manner as have the distance receptors mentioned by Sherrington; for example, some clinicians have recently assumed a direct connection between the development of the corpus Luysi and the transition from quadripedal locomotion to the erect posture. This antiquity assures for the investigator the existence of deep organic connections between locomotor processes and the most varied structural levels of the central nervous system and allows us to hope that we shall observe in the very course of the locomotor act traces of these different levels and of successive phylogenetic stratification.

Fifthly, and finally, locomotion presents an unusually stable and typical structure. This could not be assumed in advance, but it had already become apparent to us by 1934 that all the basic details of normal walking may be found in all normal adult subjects without exception, and that individual differences between subjects depend neither on differences in the structure of the locomotor act nor on the assembly of details encountered in it, but occur only in the rhythms and amplitudes of the ratios between these details. This result allowed us to build up a detailed nomenclature for the

structural elements of the locomotor act,* incorporating many dozens of stable phenomena which were invariably characteristic for each adult normal subject. The material collected by us [21] showed that the stability and generality of the structure of the locomotor act is even more widespread than we could then suppose, and that its roots may be clearly followed in early ontogeny and phylogeny in qualitative changes of locomotion, such as running or marching, and finally in a number of pathological disturbances. This will be discussed later.

All these circumstances—automatization, degree of synergy, generality, ancientness—and their stability of character make locomotor processes extremely favourable objects for investigations in the general physiology of movements.

In order to make clear in what lies the main interest in movement as a physiological topic we may recall the general features of its structure.†

The movements of an organism from the mechanical point of view arise because of changes in the conditions of equilibrium in the force field encompassing the animal's organ of movement.

In the case of spontaneous movement equilibrium is destroyed because of redistribution of tensions in the animal's muscles, within the organ of movement itself or outside it. Once the movement of an organ has begun changing both its position in relation to external forces (the force of gravity is foremost) and the degree of tension of the muscles connected to this organ, the relationships between the forces in the surrounding field continue to change until they approach to, or move still further away from, a state of equilibrium. During this process changes in muscle tension bring about a movement and the movement affects the condition of the muscles by shortening or stretching them causing further changes in their tension. We call the reciprocal connection which we have described here *the peripheral cycle of interaction*.

A mathematical analysis of similar relationships between forces (of the muscles) and movements (of the organs) shows that this form of interaction *does not presuppose a one-to-one correspondence between force and movement*, that is, that one and the same sequence of changes in forces may produce different movements on succes-

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* See *Investigations into the Biodynamics of Locomotion*, Vol. I, Ch. III, 1935.
† The thorough analysis here has relationships with our report The problem of the interrelation of co-ordination and localization (Ch. II, p. 15).

sive repetitions. This absence of one-to-one correspondence is due to the fact that the biomechanical relationships between forces and movements may be expressed in the form of a differential equation of no lower than the second order, demanding among the conditions of its solution no fewer than two values independent of the equation itself. These independent constants of integration (the original position of the organ, its initial velocity, the condition of the force field as a whole, etc.) may change from moment to moment, resulting in completely different effects from the same initial innervation.

Adequate co-ordination and a correspondence of the movement to the animal's intention are only possible under conditions in which the central nervous system constantly receives information as to the state of these independent parameters of integration and adapts its effector impulses in an exact relationship to changes in the latter. This flow of information primarily involves the proprioceptive system and provides a second ring of reciprocal connections—in our terminology *the central cycle of interaction*.

In this cycle the effector impulses change the tensions in the muscles so as to bring about acceleration of the limbs and of the system, the acceleration results in changes in positions and velocities, and the latter, like the changes in muscle tension, give rise to *proprioceptive signals*. These signals affect the course of the effector impulses introducing necessary corrections and allowing the central effector apparatus to adapt itself with *plasticity* to changing conditions at the periphery.

In this way the connection between movements and the activity of the nervous system is at once very close and very complex.

The cyclogrametric method of investigation of movements here provides invaluable opportunities for the investigator. It permits the complex registration of the movements of a whole organ or even of the whole body, giving a picture of changes on a space-time grid of coordinates for any required number of points of the body simultaneously. It allows us to pursue this description in terms of very brief time intervals by the use of shutter frequencies of the order of 150–200 per sec and higher. And what is still more important, it allows us to obtain accurate quantitative data from these pictures.

As has been said, the central nervous effector impulses do not immediately reveal themselves in a movement. The concept in

elementary textbooks that excitation of the *flexor* muscles results in flexion and that stimulation of the *extensor* muscles results in extension of the joints which they control, was seen to be erroneous even when the cyclogrametric study of movement was first begun. What is incomparably more essential and more frequently encountered is the connection between the active onset of muscular contraction (produced by the effector impulse) and the *acceleration* of the moving organ connected to the muscle. This connection was known to Fischer [43], thoroughly investigated for simple objects by Wagner [75], and taken as a starting point by our investigational group. For cases where this form of connection is applicable the cyclogrametric method gives all the data necessary for investigation, as by this means we may investigate simply, and with a high degree of accuracy, the acceleration of the movement of any given portions of the body in which we are interested. In cases of this type the curves of acceleration may give a very reliable picture of the course of effector impulses to the extremities on their final common pathway.

In more complex and general cases, where there are large-amplitude movements of complex kinematic linkages (for example, a whole arm or a whole leg), the acceleration of particular points may be quite unrelated to the course of the muscular contractions involved. We are here obliged to turn to another form of mathematical description—the *resultant moments of forces,*in joints, which can be obtained in the same way from experimental material by cyclogrametric methods of analysis. These force momenta, the method of calculation of which was first developed by us in 1928, are values which are almost directly proportional to the resultant of contractions of all the muscles around a given joint. For this reason the curves of the changes in muscular force momenta in one joint or another provide us with a picture which is extremely close to the real characteristics of the course of effector impulses in every distinct neuromuscular biomechanical group.

It is now possible to turn to locomotion, in particular to walking. The analysis of the muscle momenta in the joints of the leg in walking shows beyond doubt that the curves of muscle force momenta in walking in the majority of their details are *very close to the curves of the longitudinal component of the dynamic forces at the centres of gravity of the limb segments and systems* (i.e. for the component in the direction of the sagittal axis of the body, from back

to front, which we have designated by the symbol X). The dynamic forces which we calculated on the basis of the linear acceleration of points by Fischer's method are much more easily obtained from cyclogrametric material and are numerically more reliable than muscle momenta. The close correspondence between both forces and muscle momenta in the act of walking can be explained mainly by the fact that the actions of the force momenta are always directed perpendicularly to the longitudinal axes of the limbs. In walking, the deviation of the limbs of the leg from the vertical is not great; that is to say, lines perpendicular to them deviate only slightly from the direction of the longitudinal coordinate axis X. It follows from this that the curves of the longitudinally acting forces in the leg during walking give quite a reliable *qualitative* picture of the course of the neuromuscular effector impulses. The curves of the *acceleration* of centres of joints observed in walking, in their turn, show very close and regular correspondence to the curves of dynamic forces at the centres of gravity of the limbs. This allows us, proceeding with critical circumspection and constantly taking technical precautions, to come to conclusions as to the course of neuromuscular impulses during walking, not only from the curves of longitudinally acting dynamical forces, but also from their closest derivatives—the curves of acceleration for these same elements. The analysis of the material presented by us [21] has been carried out in this way, in cases where the calculation of dynamic forces was not possible without information on the masses of the limb segments and the locations of their centres of gravity. For running, in which we observe considerable and sharp deviations of the limb segments from their vertical axes, it was not possible to proceed with an analysis based only on the accelerations, or even, without special critical techniques, on dynamic forces, and here the conclusions of the whole work are based entirely on the calculation of the curves of the momenta.

It will appear below how complex and varied are the interrelationships in various dynamic situations in walking, between the effector impulses, their most direct reflections—the force momenta—and their more distant functions—forces and accelerations—and how many characteristic signs may be recognized in these types of connection which already allow us to reach conclusions as to the central nervous origin and character of these and other impulses. It is important here to make another point. *The structural elements*

of the dynamics of a locomotor act may certainly be deciphered by means of more or less complex mathematical and physiological alphabets which permit the revealing through them of underlying central nervous processes.

In the 1890's, in the epoch of the brilliant flowering of studies by Marey, Braune and Fischer, it was not expected that so much would come out of a study of movement. Marey was chiefly enthusiastic about his new processes of recording, by the possibilities of halting the fleeting moment and examining, by this means, what could not be seen by means of the naked eye. Braune and Fischer were concerned, on the other hand, with correcting the observations which had accumulated in preceding years and drawing parallels between them and the more accurate material which they had collected, and, on the other end, with solving some problems in the field of the theoretical mechanics of movements, regarding the leg in terms of levers, pendulums and the other accessories of general theoretical mechanics.

The main advances of our experimental group from those of Braune and Fischer must be briefly stated.* We sharply increased the shutter frequences we employed (from 26 exposures per sec, as used by Braune and Fischer, to 60–190 exposures per sec); we increased by many times the quantity of material we employed, we simplified, mechanized and verified our methods of investigation. All this allowed us to study movements in incomparably greater detail than was possible for Braune and Fischer and to obtain highly reliable data because we had more methods of verifying our experimental material and, in particular, because we used a great amount of experimental material, while Braune and Fischer were obliged to restrict themselves to three experiments on a single subject. In close connection with these differences are also the basic differences between our and Fischer's points of view.

Firstly, Fischer's approach was essentially *retrospective*, that is, he was mainly motivated by a desire to order critically the basic information available on the mechanics of the act of walking which had been gathered up to his time. Our approach may be termed *prospective*, as we were not particularly concerned with which details might be found to be reliable and which false in the work of the older authors, but attempted to provide a more reliable and

* For a more detailed discussion of this, see *Investigations in the Biodynamics of Locomotion*, Vol. I, p. 30, Moscow, 1935.

comprehensive *descriptive* basis for a subsequent broad extension of investigation into the genesis and pathology of locomotion. The main object of our investigations into locomotion from the first was to provide for future work as detailed a standard of average normal locomotion as possible, which might then be compared with whatever material might be accumulated in the future.

Secondly, Fischer was interested in the course of walking in the most general and basic terms. Therefore he ignored the details, referring a whole series of details on his photographs to errors of measurement.* Fischer supposed *a priori* that the act of walking must display a high degree of mathematical simplicity and dynamic regularity. Apparently for this reason he was satisfied with his very low shutter frequencies. Even those irregularities in the curves which could be retained on the coarse "sieve" that resulted from his low frequencies—and which, as our investigations revealed, are indicative of most important biodynamic processes—were smoothed out by Fischer and declared non-existent.

We, in contradistinction to this, gave most careful attention to these details—which on our high-accuracy, high-frequency sieve were retained much more clearly. If Fischer had *a priori* been sure that the movement of walking is maximally smooth and simple, then we, on the other hand, being aware of what complex synergy is involved in walking, expected from the very first to encounter a process of a degree of complexity which had been completely unrecognized beforehand, and which was in every case certainly impregnated with live micro- and macroscopic details, just as is living organic tissue. Our expectations in these respects were fulfilled in the highest degree. "The biodynamic tissue" of live movements—of locomotion—appeared to be full of an enormous number of regular and stable details. In the course of one complete cycle of movement —one double step—each of the moving organs appeared to participate in a complex melody of scores of dynamic waves which followed each other with precision and regularity. Amongst these there were large and powerful waves, for example, the waves of the forward and backward thrusts which would have been visible even through Fischer's weak "telescope" if he had not smoothed them out of the curves together with the "dust-spots" and waves of the second order and, finally, the smallest objects which are located

* See *Investigations in the Biodynamics of Locomotion*, p. 11, 1935.

at the very limit of the resolution power of our present technology. The transition between stars of the first magnitude and the faintest visible objects is such a gradual transition, that without any doubt a multitude of stable particulars in locomotor processes are still invisible to us; there is considerable reason to suppose that it is precisely these ultratelescopic objects—these still unresolvable details of biomechanical tissue—that will seem the most interesting in the future.

All these circumstances determined the third and, in principle, the most important aspect of our approach to the study of locomotion. We refused to theorize about our object of investigation in advance by forcing it to fit one or other analog in the field of general mechanics. We regarded the locomotor process as a living *morphological object* of inexhaustible complexity and set as our primary task the necessity of observing and describing it as closely as possible.

As early as 1928 [15], I put forward in general terms the concept that the movements of a living organism could be regarded as morphological objects. That they do not exist as homogeneous wholes at every moment but develop in time, that in their essence they incorporate time coordinates (in ways different from tissues and organs, for example), and that they are in no way dissimilar to objects in the morphological field of investigation. On the contrary, the concept that movements are in many respects similar to organs (existing, as do organs, in a system of space-time coordinates (x, y, z, t)) appears to be extremely fruitful, particularly when the discussion concerns such stable and general forms of movement as locomotion.

The basic vital properties which exist in the movements of living beings clearly confirm their close analogy to anatomical organs or tissues. Firstly, a live movement *reacts* and secondly it regularly *evolves* and *involutes*.*

I noted and described the former of these properties as early as 1924 [8, 9]. Studying the biodynamics of movements involved in

* The reactivity of the live structure of movements cannot be simply mechanically related to the reactivity of live organic tissues which take part in the given movement. The discussion does not concern the point that movement is a basic substrate—this would be completely false—but that the forms of the reaction of the material substrates of movement, which determine by their existence the course of a living movement, have quite particular qualitative characteristics.

cutting with a chisel I was able to show that it is impossible to alter selectively any one given detail in this movement without affecting others. If, for example, the trajectory of the elbow is slightly altered, the form of the trajectory of the hammer is also unavoidably changed, as are the relationships between the velocity of the swing and the impact, and between the velocities of the wrist and of the hammer head, and a whole series of other nuances of the movement.

In subsequent years it was possible to establish from material obtained on walking that the reactivity of movements is extremely selective. Movements react to changes in one single detail with changes in a whole series of others which are sometimes very far removed from the former both in space and in time, and leave untouched such elements as are closely adjacent to the first detail, almost merged with it. In this way *movements are not chains of details but structures which are differentiated into details*; they are structurally whole, simultaneously exhibiting a high degree of differentiation of elements and differing in the particular forms of the relationships between these elements. This justified the analogy which I made earlier between the characteristics of living movements and tissues, calling them both biodynamic tissues.

A second property of the movements of a living being has been established for a long time—they develop and involute. However, the problems of the ways in which they develop, and the stages they pass through in this process, etc., have been very little investigated. We will give some account below of the most important results obtained in this direction.

2. The Basic Structural Components of the Locomotor Act

We shall discuss in general terms the basic biodynamic characteristics of the process of walking [19]. These must serve as points of departure for further analysis.

The movement of walking consists, for each leg, in alternations of periods of *support* and *swing-through*. The swing phases are of shorter duration than the periods of support (for running the pattern is inverted), for which reason there are intervals during which one leg has not yet completed and the other has already begun its support phase. We call these intervals periods of *double support*.

The dynamics of the legs in their interactions with the supporting surface have their most clear-cut reflection in the behaviour of the centre of gravity of the whole body. In fact the forces which operate during walking at the centre of gravity of the whole body are equal in magnitude and opposite in direction to the forces which are applied to the supporting surface by the supporting leg or legs. By the principle of the equality of action and reaction, these forces in the legs are, in their turn, equal and opposite to the support reaction,
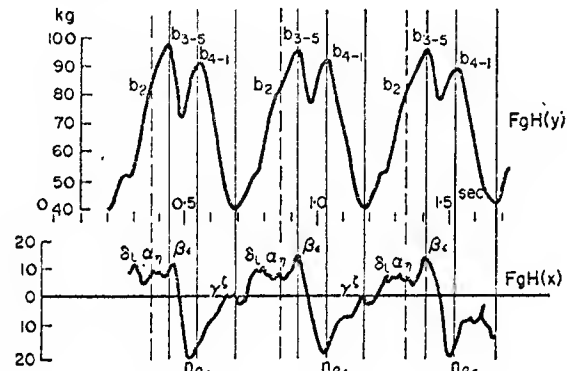

FIG. 22. Curves of forces at the centre of gravity of the whole body during normal walking. Above: vertical components. Below: horizontal components.

that is, the reaction of forces in the surface supporting the body of the walker. For this reason the curve of the dynamic forces at the centre of gravity of the whole body is exactly the same as the curve of the support reaction, that is, the curve of the interaction between the lower extremities and the supporting surface.

Graphs of dynamic forces at the centre of gravity of the whole body (Fig. 22) are among the types of evidence which may be quite easily obtained from live movements by the cyclogrametric method. These graphs incorporate a series of clear-cut and reliably stable elements which are evident in all normal human subjects without exception. The vertical component of stresses in the centre of gravity of the body as a whole $F_{gH}(y)$ displays two high peaks, h and v, which we have termed the backward and forward thrusts (h—*Hinterstoß*, v—*Vorderstoß*). The rear thrust is delivered by the leg, standing behind at the beginning of the period of double support;

the front thrust is delivered towards the end of this period, about 100–200 msec later by the front leg. In this way every period of double support in walking begins with a rear thrust (with one leg) and ends with a front thrust (with the other leg). The support period for each leg begins with its front thrust and ends with the rear thrust. The entire sequence of events is clearly represented in Fig. 23.

Shortly before the rear thrust the leg that is behind delivers another vertical thrust of varying magnitude—the auxiliary thrust h'. The middle of the single support time—that moment when the swinging foot moves past the supporting foot—corresponds to the principal minimum m of the vertical component $F_{gH}(y)$. At that moment the pressure of the foot on the supporting surface is significantly less than the static weight of the walking subject, whereas, at the moments of the two principal thrusts h and v, it is significantly greater than this weight.
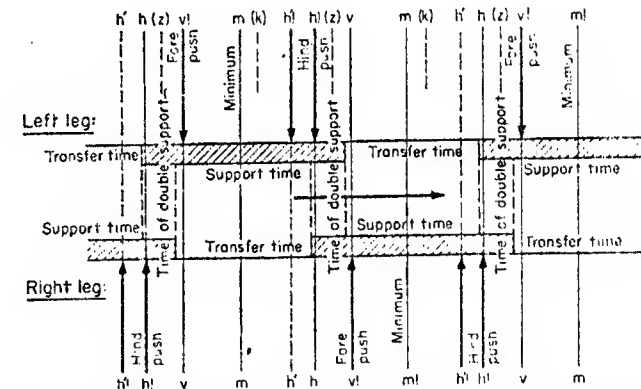
FIG. 23. Diagram of alternation of principal thrust forces in normal walking (the figure is corrected by data obtained from recent studies by O. Saltzgeber).

The longitudinal components of the forces at the centre of gravity of the whole body $F_{gH}(x)$ (Fig. 22) are significantly less constant than the vertical components in form, though not in the dynamic elements which they incorporate. These latter always appear in a strict sequential order varying only in their magnitudes and in the nuances of their rhythmical interrelationships. The most significant

in amplitude are the direct (that is, forward-directed) thrust β_ϵ which occurs almost simultaneously with the rear thrust h, and the reverse (directed to the rear) thrust $n_{\beta\epsilon}$ which appears a little before the front thrust v. If we examine both components in their entirety, that is, if we consider the forces at the centre of gravity as a vector, then the alternation in the waves which has been described will be visible in this way: The rear thrust manifests itself at the centre of gravity as a vector directed forwards and upwards which displays a small oscillation forward (β_ϵ) immediately after its maximum (h); the front thrust is a vector directed upwards and backwards ($n_{\beta\epsilon}$) which deviates slightly further forward at the moment of its maximum (v).

The intermediate stable elements of the curve of the longitudinal components $\gamma\zeta$, $\delta\iota$, χ, $\alpha\eta$, are of great value in the co-ordination of the movements of the legs and determine all the details of these movements, but their relation to the movements of the centre of gravity of the whole body is not at present very clear. The wave α_η occurs close in time to the auxiliary thrust h'.

The curves of the dynamic forces at the centre of gravity of the segments of the leg and at the centre of gravity of the whole leg may be considered as indicators of the locomotor structure on one side of the body. While the curves of forces at the centre of gravity of the whole body F_{gH} show the periodicity of a single step and reflect in equal measure the dynamics, now of one, and now of the other side of the body (this is the reason for the two-letter symbols which I have given to elements of the longitudinal components), the curves for the segments in the leg display periodicity over a double step. As examples in the present brief discussion of the curves of forces for the legs we may consider the force vector for the thigh (F_{gf}) which is shown in Fig. 24 as curves for the vertical $F_{gf}(y)$ and longitudinal $F_{gf}(x)$ components. This vector is the richest of all the force-vectors in the legs in structural details, for which reason we draw attention to it. The vector for the thigh is, for two reasons, in a particularly favourable position to allow a large number of biodynamic structural details to appear in it. Firstly, the thigh is located at the centre between the "shin–foot" system at one end and the trunk at the other so that it is simultaneously affected by the operation of both systems and is an arena for the interplay of reactions of support and of forces which originate in the trunk and the contralateral leg. Secondly, its moment of inertia in relation to the

hip joint is significantly less than the moments of other distal segments relative to this joint, i.e. the lower leg and foot; for this reason the thigh reacts more sensitively to all the nuances and shifts in the thrust impulses communicated to the leg by the hip musculature.
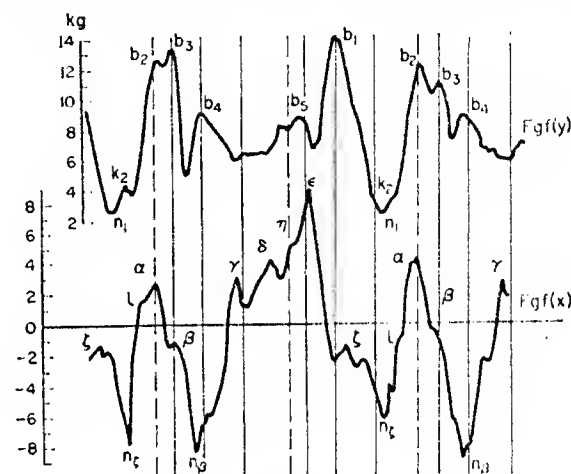
FIG. 24. Force curves at the centre of gravity of the thigh in normal walking. Above: vertical components. Below: horizontal components.

The vertical component of forces at the centre of gravity of the thigh $F_{gf}(y)$ (Fig. 24) is made up of an alternation of high groups of peaks with the raised plateau of the support period, and the deep troughs (n) of the transfer period. The group of peaks after the swing period minimum includes the peaks b_2, b_3, and b_4 if we do not consider the small irregular wave k_2 at the very bottom of the trough n_1. The peak b_2 coincides in time with the auxiliary thrust h' and is apparently caused by it. The peak b_3 is an echo of the rear thrust h of the opposite leg, that is, it directly precedes the beginning of support by the given leg. The peak b_4, which is always much lower than both the previous peaks, is the effect of the operation of the front thrust by the given leg. The powerful wave of this thrust is transmitted through the thigh, and the small peak b_4 is a part of this thrust deposited into the curve of the thigh itself.

The support plateau is terminated by the poorly differentiated low group b_5 (sometimes b_5–b'_5) reproducing the thrusts h' and h on the given side in the same order as b_4 reproduces the front

thrust. There then follows the high wave b_1—the reflection of the front thrust on the opposite side—after which comes the swing-phase minimum n_1.

And so the vertical component of the forces F_{gf} incorporates the main waves b_2, b_3, b_1 corresponding to the main thrusts on the opposite side and the lower peaks b_4 and b_5 corresponding to the same thrusts on the given side. All these elements are stable in normal adult subjects and are repeated in the same order in the curves for the action of forces in the shin and the leg as a whole. Except for these force elements, nothing stable and characteristic is observed in the curve $F_{gf}(y)$ and in the similar curves $F_{gs}(y)$ and $F_{g(fsp)}y$.

In this way the vertical components of forces in the leg during walking basically incorporate only elements which reflect the struggle of the moving organism as a whole with the force of gravity: the after-effects of its supporting thrusts and the reflections of thrusts on the opposite side. This completely agrees with what has been said above in section 1; the manifestation of local muscular activity in walking must be observed mainly in the forces visible in the curves of the longitudinal components, while in the vertical components we find only very remote and generalized phenomena directly related to the integral dynamics of the centre of gravity of the whole body.

For all these reasons it seems that the most comprehensive and interesting neurodynamic material available to us must be the *curves for the longitudinal components in the legs*, and this expectation is fully verified. We may recall the nomenclature which we have adopted for the longitudinal components of forces.

The most distinct direct (inclined forward) force waves of the curve $F_{gb}(x)$ have been indicated by the first letters of the greek alphabet in their sequential order: α, β, γ, δ, ε, ζ. We have designated the reverse waves by the symbol n with the addition of an index to indicate the prior direct wave, for example, n_ε is the reverse wave immediately following the direct wave ε, and so on.

This nomenclature could not be retained in such a simple and schematic way. New smaller waves and previously unnoticed details, etc., are constantly being observed. For this reason we now regard the entire nomenclature we have given as only a series of proper names and we do not seek greater rationality in them than may be found in geographical or astrophysical terms.

The support period of the legs (see Fig. 24) commences with the very marked reverse wave n_β. This wave occurs immediately before the front thrust of the given leg and essentially represents the braking effect of the planting of the foot on the supporting surface. In the curve for the forces at the centre of gravity of the body at this moment we observe the appearance of the reverse wave n_β.

During the course of the support period itself there is a gradual stepwise rise in the curve $F_{gf}(x)$. It displays a small rise close to the zero level, γ (between $v!$ and $m!$),* a direct wave δ of moderate amplitude height, another higher region with poor relief η (close to h') and, finally, a large direct peak ε at the moment of the rear thrust on the same side.

The gradual jagged rise γ–δ–η corresponds to the steady increase of the horizontal velocity of the thigh, particularly its distal end; that is, it reflects the increase in the activity of the supporting leg pressing on the ground. The wave ε, the last and distinct direct peak of the curve $F_{gf}(x)$, occupies precisely the same dominant position in the curves for the shin and foot, and sharply falls after the rear thrust. From this point on, that is to say, from the beginning of the swing period on, the forces in the thigh display a course which is quantitatively different from those at the centres of gravity of the whole leg and its lower segments, but there nevertheless remain the same structural elements common to all moving organs, which are only disposed differently in relation to the axis of the abscissa (Fig. 25).

The direct element of the curve $F_{gf}(x)$ following immediately after ε is the jagged region ζ located between the front thrust v and the minimum m for the opposite leg. In the curve for the centre of gravity of the whole leg this region is located a little above the zero level (in the direct waves), whereas in the curve for the thigh it lies below zero (in the reverse waves). It is preceded in the curve $F_{gf}(x)$ by the reverse wave n_ε and it terminates in another reverse wave n_ζ. The reason for the different disposition of the region ζ in different curves is explained below; at present it need only be said that the reverse waves n_ε and n_ζ represent the braking effect, which begins at this point, on the forward velocity of the leg (and of the knee joint) which is accompanied by increases in the longitudinal velocities of the foot and the shin. The muscle forces in the hip and knee joints

* The exclamation mark is used to designate the main thrusts on the same (ipsilateral) side of the body.

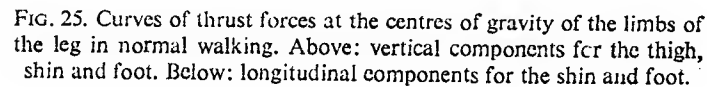FIG. 25. Curves of thrust forces at the centres of gravity of the limbs of the leg in normal walking. Above: vertical components for the thigh, shin and foot. Below: longitudinal components for the shin and foot.

during the period represented by the region ζ are *extensory* (Fig. 25) so that the braking of the thigh is reactively provoked by peripherally operative forces.

Following n_ζ in the curve $F_{\theta f}(x)$ there appears a high and compact group of waves, the summit of which constitutes the wave α. This direct wave only exists in the thigh; for the shin and the foot we have at this point the reverse wave n_α. At that moment there are also reverse waves in the curves of the force moments at the hip and knee joints (Fig. 29). In this way the wave α for the thigh is not a resultant of muscle action, but is reactively produced by the periphery in the same way as is the braking effect on the knee in area ζ which has been noted above. The wave α and its functional pair n_α correspond closely in time with the supplementary thrust in the opposite leg h'.

Almost merging with α in the curve for the thigh we find the trace of a sharp peak β (the phase h in the opposite leg), in which, however, all the signs indicate quite another process than that at α. Firstly, this rise is observed in the form of a direct peak in all curves for the leg while there is no trace whatever of α in the curves for the shin and the foot. Secondly, as will be shown below, the whole history of the development of this peak β is radically different than that for α. By these means we can ascertain that it is related to its neighbour not functionally, but as "an optical pair".*

This, in its most general features, is the framework of the structure of the longitudinal forces in normal adult walking. We may deduce from the inventory of the primary properties of the force impulses, which determine the stepping movements of the leg in walking given above, that these are certainly not limited to one simple pair of impulses, a forward impulse and a backward impulse, for each double step. Examples of such reciprocal impulses might be, for instance, ε and n_β which operate practically simultaneously in both legs in opposite directions to one another. The facts of the matter make evident that this most simple pair will not in any way exhaust the data. The multiplicity of elements interacting regularly with one another and making up a complex and idiosyncratic rhythm of alternation gives to the dynamics of each separate step a radically different physiognomy from that which may be observed in the simple stepping reflex in a decerebrate preparation. All these ele-

* *Translators note:* The distinction made in astronomy between physical and optical pairs in the case of double stars.

ments are strikingly constant and general, they occur in precisely the same unchanging sequence in all the longitudinal force curves for all the elements of the leg and the trunk in normal walking, they retain this constancy of structure in all normal subjects and they remain the same even in a whole series of central nervous system disorders. Further these very structural elements, in this precise sequence, are retained in a form of locomotion as qualitatively different from walking as running; and gross peripheral disturbances of structure, such as amputation, are necessary before they are lost to any significant degree. All this indicates that the structural elements of muscle action which have been described above are not in any way accidental, that they are of essential co-ordinational significance for the locomotor act and that to all appearances they must consequently have a peculiar genesis, history and basis in the central nervous system or elsewhere. The confirmation of all these suppositions is the basis for the material discussed in this work [21]; in subsequent sections we shall examine the facts which relate to these topics.

3. The Genesis of the Biodynamical Structure of the Locomotor Act

The first fact revealed to us by our study of the ontogenesis of walking and running in the child was that *biodynamic structures live and develop.*

All the numerous elements which were briefly described in the preceding sections, and which were there irrefutably shown to participate in the co-ordinational formulation of an act of locomotion, are absent from the walk of a child which has just started to walk by himself. Considering the longitudinal acceleration curves of the child, in the first days of independent walking only the direct wave ε is present in the leg as a whole; the reverse wave n_α in the foot is accompanied by its functional pair α in the thigh; and the region for the hip joint is, as we see, entirely different from the adult ζ. There are no traces of β, γ, δ, η, θ, or ι. This picture is retained during the whole of the 1st year of walking, that is to say, until nearly the 2nd year of life.

In other words, in the whole of the muscular-dynamic inventory of the child in the first months of the development of his walk we

may observe only one pair of independent muscle impulses ε and n_α,* the identical simplest reciprocal pair which we have described in the previous sections and which were believed by physiologists of the last century to explain the entire muscular dynamics of walking in adults. The other two waves which are observed in this early stage of ontogenesis have essentially a peripheral origin; namely, the purely reactive-mechanical α which arises in the thigh as a reaction to the active muscle stress n_α, and the reactive pair $\zeta - n_\varepsilon$ for which the same is true. The impulses ε and n_α develop first, and initially there are no others. I should term this level of development the *innervationally primitive* stage.

The following elements of the biodynamic curves develop much later: within 2 years of birth the infant has, besides the curves mentioned above, the waves γ and η in the thigh and signs of the beginning of the development of β in the knee and the ankle joint. These new elements are not yet clear-cut, and where, for example, tempo is increased, they have a tendency to disappear.

The whole inventory of dynamic waves develops very slowly, being complete by about the 5th year. The separate elements very gradually change over from the group of those which are not constantly encountered, and which are not observed in every step (γ) to the category of those which are constant for slow tempos, and finally to the category of unconditionally constant signs. The development of the adult forms of the structural elements is also completed slowly, and, for example, even by the 4th year the "childish" ζ has not fully given place to the adult version.

In the first place, all this is evidence that the gradual appearance and consolidation of new structural elements is not in any way related to the elaboration of elementary co-ordination and equilibrium in walking. By the age of 3 or 4 the child is not only able to walk without difficulty, but can also run, hop on one leg, pedal a tricycle, etc. This means that the mechanisms of co-ordination for all types of locomotor movements and for the maintenance of equilibrium have been thoroughly elaborated for some time, whereas the inventory of the dynamic impulses for normal walking is still far from complete. A little later on we shall see that the nervous mechanisms of elementary co-ordination and the maintenance of equilibrium are illuminated in quite another way by the curves obtained for children. The basic structural elements which we have

* Not n_β as β still does not exist.

just been discussing clearly have some other significance and are related to finer details of motor co-ordination.

The development of the structural elements of walking is completed in a manner which is far from direct. On the contrary, during ontogenesis a whole series of redundant signs which are not peculiar to adults appear, to disappear again at adolescence. These childish elements appear very early among the vertical components. By the 1st year of independent walking, while the child has only b_1 and b_3 among the whole range of adult components, there are also apparent, alternating with them, the "infantile" waves k_1 and k_2. The second of these may also survive in adulthood in the form of a step k at the bottom of the wave b_2, although the homology of both these forms has not yet been rigorously proved; k_1 certainly disappears by the age of 7 appearing again only in cases of amputation in the transverse components of the forces $F(z)$. The infantile mechanical-reactive wave ζ in the thigh appears, as we have seen, very early and is maintained during the course of the entire 1st year of walking. It then falls away like a milk-tooth; the adult innervationally reactive form of ζ develops in its place only in the 4th–5th years of life.

An extremely interesting overemphasis of structural details occurs in the period of development between 5–8 years. During this period all possible variations of θ, η and ι often occur with very large dimensions; the vertical infantile thrusts k_1 and k_2 also attain very significant dimensions as do the horizontal details γ and ι which are still bound in synchrony to them. This overabundance energetically involutes between 8 and 10 years, but even by the age of 10 the process of formation of the adult structure has not been entirely completed.

In the course of the development of the biodynamic structure of walking there also appear qualitative deviations of another type which cast light upon the gradual mastery of the mechanisms of co-ordination and equilibrium. In the very first days of independent walking the vertical components of forces at the centre of gravity of the head of the infant already appear to be completely ordered and invariable from step to step, although primitive in form—only the waves b_1 and b_3 may be discerned in them. Meanwhile, the *movements* of the head (the curves $S_c(y)$) are extremely chaotic, uneven and involved. Towards the age of 2 the curves of the vertical forces for the head are gradually enriched by new waves and in ex-

tremely close connection with these the curves of *movements* $S_c(y)$ become increasingly more simple and stable. We may relate this to the fact that in various children we observe less intervariance in the curves of forces and accelerations of their heads than in the extremely diverse and individual curves of displacements.

An explanation of these phenomena follows directly from the basic conditions of the structure of movement which were discussed above. The given curve of changes in muscle forces (and it follows, in the simplest cases, of acceleration) cannot alone entirely determine the resulting movements as independent parameters of integration.*

The effect of these independent parameters is stabilized in the normal development of the central nervous system by the proprioceptive apparatus; this signalling compels the motor areas of the central nervous system to adapt the form of their effector impulses. If the proprioceptive impulses are interrupted, as occurs, for
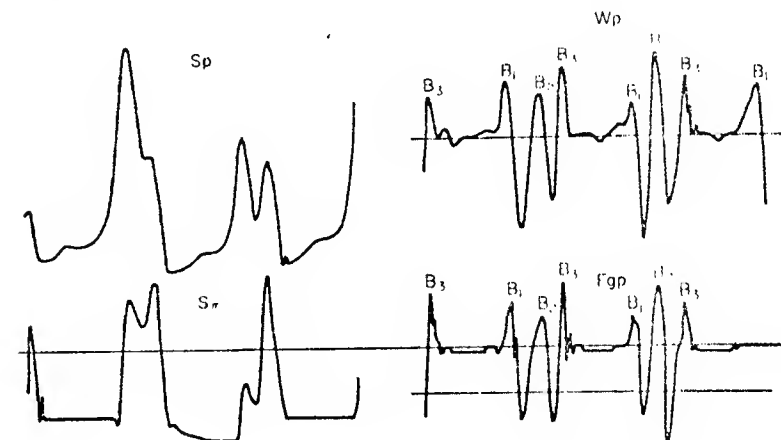
Fig. 26(a). Left side: vertical translations of the ankle and the toe end. Right side: vertical accelerations of the ankle joint and vertical efforts in the foot during two consecutive paces in walking of a patient with tabetical ataxia. It can be seen clearly that a moderate variability of accelerations and efforts in consecutive cycles of movement of a tabetic patient can result in strikingly different forms of translation curves in the same cycles.

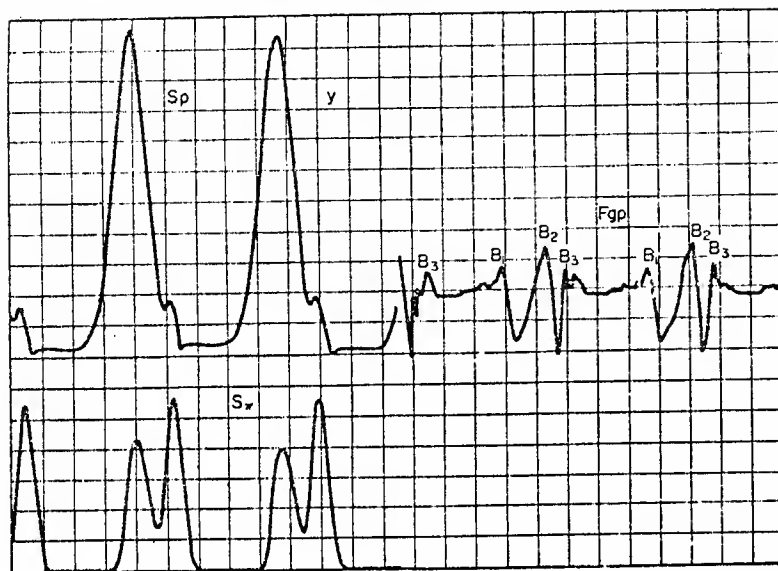* Mathematically and not in a Sherringtonian sense.

FIG. 26(b). Left side: vertical translations of the ankle and the toe end. Right side: vertical efforts in the foot during two consecutive paces in walking of a normal subject. The curve of efforts shows only a slightly lesser variability of cycles in comparison with those of the preceding figure, while the translation curves are absolutely identical from pace to pace.

example, in the classic case of tabes, we obtain as a result extremely regular and constant successive cycles of *forces F* and *accelerations W* with completely disordered and dissimilar cycles of *displacements S*. We have material on tabes among our unpublished data which provides very clear examples of this type (Fig. 26). We may deduce from this that the principal and most general symptom of disturbances in proprioceptor signalling (proprioceptive ataxia) is the *disturbance in successive cycles of the constancy of S* with (sometimes marked) retention of *constancy of F and W*.

In small children we are dealing, naturally, not with disorders in proprioceptive signalling, but only with the slow and gradual appearance of the mechanisms of adequate response to this signalling. In cases where this mechanism has not yet been built up we may observe the ataxic symptom which we have described—the regularity of *W* and chaotic disorder of *S*. In this stage of onto-

genesis the spontaneous effector impulses are consequently already developed (*W* is in order) while the innervational-reactive impulses do not operate in conjunction with them.

In locomotion of children there are a whole series of phenomena of this sort which are clearly observable at first, and later grow fainter and fainter. In children who have only just begun to walk there is as a rule no constant correspondence between dynamic phases and the positions of the body. Their phases, appearing in successive steps as the phase of one and the same force waves, are quite unlike each other. For adults, on the other hand, there is an exact repetition of positions in simultaneous dynamic instants (see Fig. 27(a)). Further, for some dynamic waves, for example ζ, the connection between positions and phases is extremely stable and is not even destroyed by very gross changes in gait. The absence of a similar correspondency in small children is naturally an indication of the same relationships seen in the chaotic forms of the *S* curves; the absence of correct response to proprioception.

In slightly later stages of childhood development when the most elementary mechanisms of locomotor co-ordination have already been mastered, the same symptom of inadequate mastery of proprioceptive signalling appears in a fainter and partly transformed aspect. The situation is the same in the case of the ζ wave, which, when all is considered, is one of the most complex and enigmatic of all the co-ordinational waves. T. Popova observed that the height of the ζ wave in children between the ages of $1\frac{1}{2}$ and 3 years is in very close correspondence with the length of the stride and that apparently the inadequate participation in one or another separate step of the main ε impulses is compensated, so that a step may be correctly made by the incorporation of the ζ wave. In some cases, ζ in this context considerably overshadows the basic ε impulses and in this pattern of walking waves appear which vary considerably in magnitude from step to step. This observation discloses a connection between proprioception and the effector system, but now in a new scheme. Because of the inadequacy of the motor responses, which are not yet proportionally related to the amount and the exact graduations of the force ε (the auxiliary waves δ and η! are undeveloped), unequal steps are obtained for constant values of ζ, while for steps of constant length variations in ζ are necessary. In the adult norm it is both the case that ζ are of constant value and that steps are of constant length; this means that even *before*

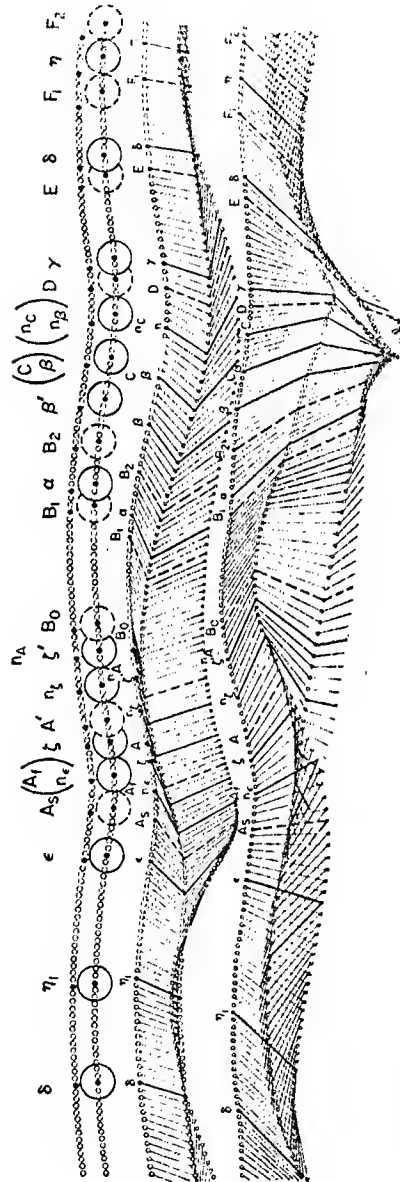Fig. 27(a). Successive positions of the right side of T. Ladoumeg's body, taken at a frequency of 187/sec in experiment No. 731. Heavy lines mark phases of the movement corresponding to characteristic dynamic phenomena. Continuous heavy lines indicate longitudinal dynamic elements. Heavy dotted lines indicate vertical elements.
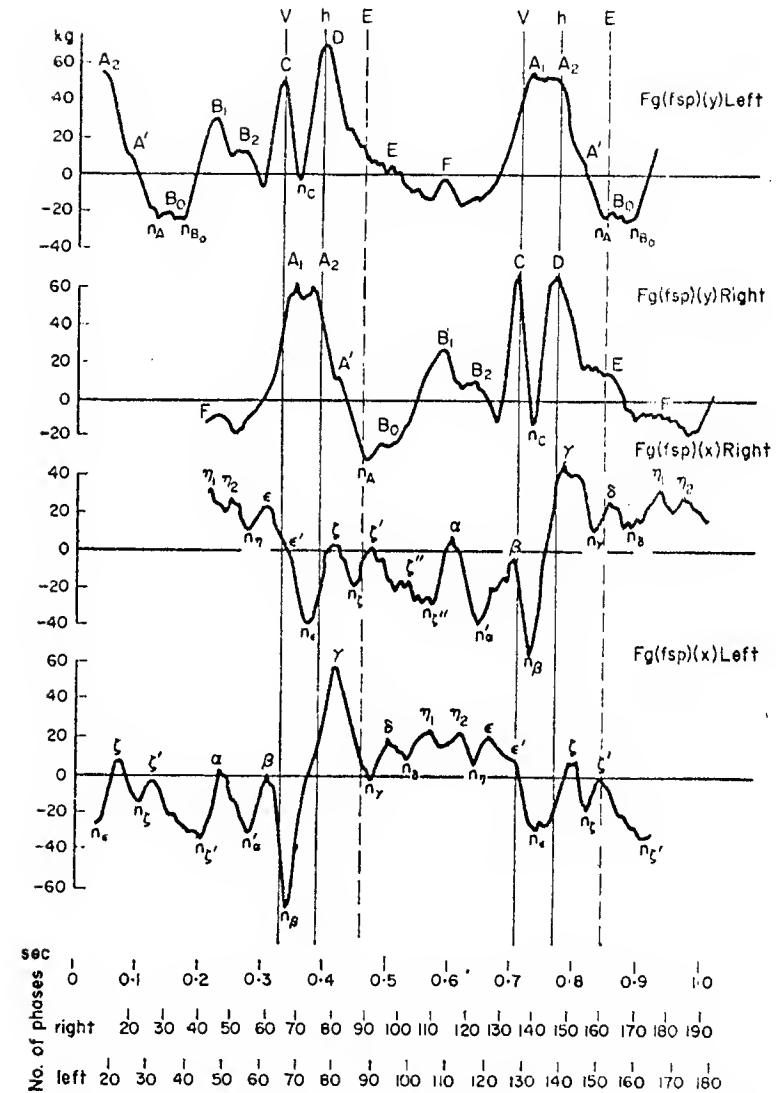
Fig. 27(b). Forces at the centres of gravity of Ladoumeg's right and left legs. Standard terminology.

the completion of the main impulse ε an exact regulation of the direct longitudinal forces on the basis of propriosignalling is necessary in carrying out steps of constant metric proportions. This preparatory regulation has not yet been developed in the child and it depends on subsequent compensation including the *termination* of the impulse ε. The proprioceptive activity is still inadequate to allow metric *planning* of movements but is capable (in distinction to the very earliest stages) of introducing metric *correctives.*

The evolution of the locomotor act involves nearly the whole of childhood and extends almost to the beginning of puberty. The last stage through which it must pass, which begins to be observable only after the age of 5, and which disappears only after the age of 10, is the conversion of an undifferentiated collection of biodynamic elements into a determinate structure. All the structural elements of walking have developed by the 5th year and, as has been said above, are still encumbered by a whole collection of infantile peaks and hillocks for the next few years. However, at the beginning of this stage of development all the "teeth" in the curves, both the "adult teeth" and the "milk teeth" although they are already located in the correct sequential order, have not yet as a whole adopted the *form* which is characteristic of the adult curve. This form is finally apparent when regular and constant proportions are established between the elements of the curve, when the smaller "half-tone" elements merge and are effaced, and the larger elements emerge into dominant positions. It is only then that the last and highest stage of development of co-ordination is completed: the displacements (*S*) become regular and of equal lengths, and here neither curves of forces (*F*), nor accelerations (*W*), necessarily vary in order to compensate for irregularities (as it were, *post factum*, in proprioception), so that it is possible to maintain a unity of movements without violating the unity of the force curves (as a result of proprioception *ante factum*).

A similar picture may be observed in the *running* of children. In giving an account of the adult run, we have been able to show that running considered as a *neurodynamic* structure displays many incontestable signs of similarity to walking. This relationship is clearly marked in an analysis in depth of running, and is in sharp contrast to running regarded as a *biomechanical* structure in which respect it is in many ways exactly opposite to walking. The problem of moving the body through space is solved in almost directly op-

posite ways in running and walking and a whole series of features of the structure of innervational processes undergoes basic changes in running in comparison with walking, notwithstanding the incontestable common genesis of both processes in the nervous system. This common origin may be studied and proved with the greatest clarity in the context of the evolution of running in children, where we clearly observe the common operation of locomotor structure as well as the gradual course of their biomechanical and neurodynamic *divergencies.*

In the very earliest phases of development of locomotion (in the 2nd year of life) it is impossible to observe clear differences between running and walking in the child. His run is quite free of the most characteristic sign of a true run—the interval of flight—and is only very slightly different from walking. Only a few dynamic elements similar to those encountered in true running appear at the proximal ends of the legs while the distal ends still present the picture characteristic of walking. All these changes are concentrated in the *support period* in the structure of which all the first signs of divergences are incorporated.

Very gradually, during the 2nd and 3rd years of life, parallel with the mastery of new elements in the curves for walking, we find the development of divergencies in the running curves. The front and rear thrusts of the supporting leg (*C* and *D* in Fig. 28(a)) are shifted nearer in time as compared with those observed in the walk of a given child; the longitudinal force waves γ and δ develop in place of the older primary wave ε which is reduced in running and changes its position from the support group γ-δ-η to the transfer group ζ-α; we also observe the first traces of *flight*. It is an interesting fact that the curves of the vertical dynamic components diverge earlier than the curves of the longitudinal components (Fig. 28(b)). If we remember that the former are closely concerned with the integral dynamics of the organism and with its biodynamic activity in its struggle with the force of gravity, whereas the latter mainly reflect the internal more intimate structure of the force impulses in the given extremity, an explanation of this phenomenon may be attempted. It seems to me that the delay in the appearance of divergency in the case of the longitudinal curves in comparison with the vertical is a sign that the reorganization of the movement begins with its biomechanics, that is to say, with the *peripheral parts* of the process (the reorganization of the support interval, the organ-
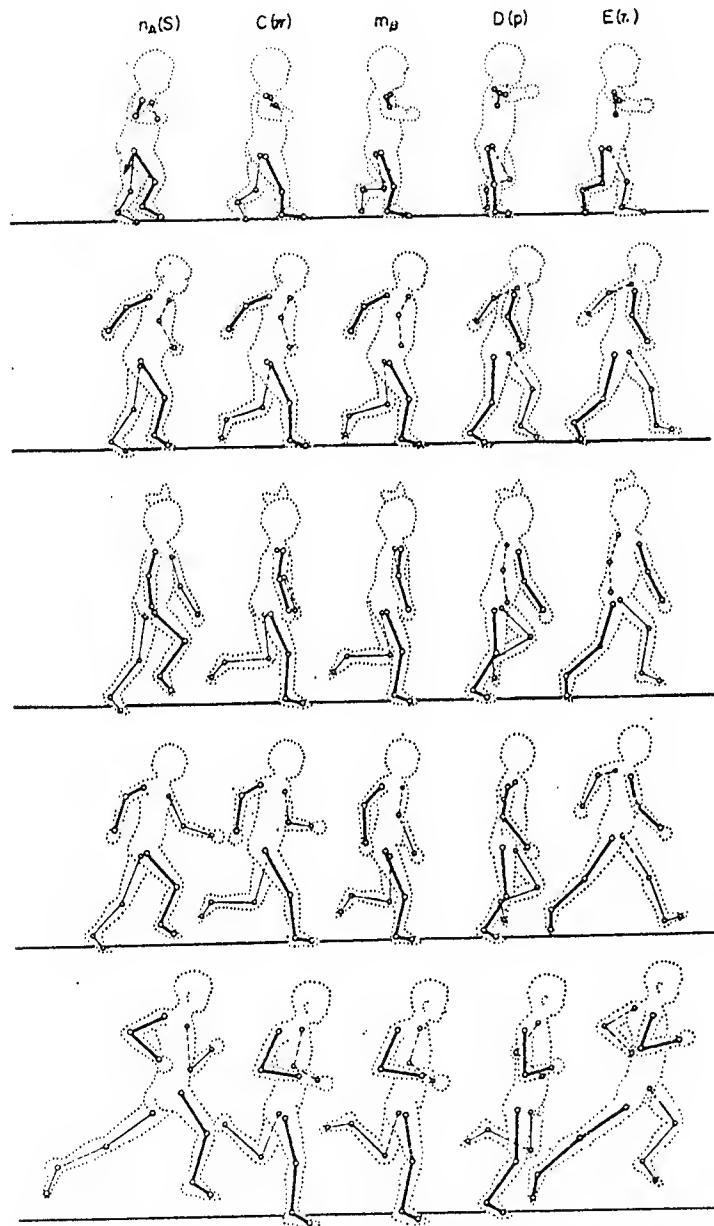
$n_A(S)$ $C(\pi)$ m_β $D(p)$ $E(\pi.)$

FIG. 28(a). Schemes for positions of the body during phases of the step. n_A, downward push in the thigh of the rear leg; C, thrust to the rear by the rear leg; m, limit of raising of the knee to the rear; D, thrust to the rear; E, the last dynamic element of the support period.

ization of the phase of flight, etc.); this biomechanical reorganization sets new problems for the central nervous system, to which it gradually adapts, mirroring that adaptation in subsequent changes in the longitudinal dynamic curves. This secondary character of *central divergency* is also very marked in another phenomenon which will be discussed a little later, that is, in the diminution of the
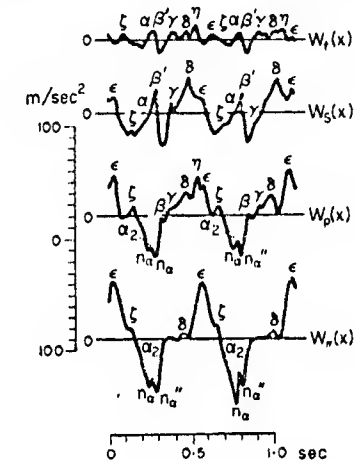
FIG. 28(b). Longitudinal acceleration of the hip (f), knee (s), and ankle (p) joints and of the point of the foot (π) during walking of a child aged 3 years and 5 months. (T.P.; experiment No. 963.) The support period is indicated by horizontal lines at the bottom of the graph.

amplitude of the longitudinal force curves in the qualitative development of running with increasing age.

Though it was necessary in the first stages of the development of running to use care in determining differences from walking, in subsequent stages (from 2 to 5 years) the basic properties of running are quite incontrovertibly apparent. In this age group the organization of the *transfer period* in running has already begun (firstly the latter half of transfer, then the former). In particular, during this stage of development dynamic novelties appear in the transfer period and, curiously, the overwhelming majority of them appear at the *proximal* points of the lower limbs, while the distal points do not display noticeable signs of divergency for some time. From 2 to 5 years the longitudinal curves for the thigh already display the typical structure of the running swing-phase period in its

entirety, while the curves for the foot are still not differentiated from those obtained for walking, even in respect to the support interval.

This prevalent course of evolution and of divergency from above to below, from proximal to distal points, leads to an interesting physiological generalization. It is very improbable indeed that the nerve dynamics of the distal musculature are so sharply different (by a whole year of development) from the dynamics of the proximal muscles. It is much more probable that there is another explanation here. The proximal ends of the legs (for example the hip joints) are surrounded by far more massive muscles than are the distal ends (the feet), while at the same time the moments of inertia of the former are much less than the moments of inertia for the latter. For this reason the muscles of the hip can move the upper sections of the limbs much more easily than the foot, since to move the foot they must oppose the inertia of the entire leg from top to bottom. There is also the fact that the (relative) velocities are higher as a rule for distal than for proximal parts, so that the kinetic energies of the former are higher and it is more difficult to overcome them. The distal parts play roles reminiscent of heavy flywheels in relation to the legs as a whole.

It follows that the nerve effector impulse at any given strength of its operation appears far more easily in the proximal curve and is mirrored there in the form of observable dynamic waves, because it does not have to overcome all the inertial resistance of the distal system. In order to be perceptible in this latter system, the effector impulse either must be very strong or must coincide exactly with the moment when conditions in the distal system are particularly favourable for its appearance. It is still difficult to say what these particularly favourable conditions are, and here a wide field of investigation is opened. It is possible that we have here simply a convenient position of the extremities which offers the muscles the most favourable biomechanical conditions of operation; it is possible that this most opportune moment is a critical moment in the velocity of the limb when the inertial resistance is least perceptible; finally, it may be the case that it is at this moment that the degree of excitability of the muscle apparatus is most receptive because of some favourable concurrence of proprioceptive signals (this latter hypothesis may be successfully tested by electrophysiological techniques). In one way or another the control of the distal

parts demands a greater deftness, a higher degree of co-ordinational technique in respect to the skill of selecting the optimal moment to give just the right impulse at just the right time. If this moment is lost, even by a fraction of a second (it must never be forgotten that all processes in running are measured in terms of hundredths and thousandths of a second), then the impulse will fail to penetrate; that is to say, it will not produce any noticeable effect at the periphery.

We must stress here that we are not discussing small co-ordinated movements of the distal sections such as finger movements, but global general displacements of distal portions of the body of the extrapyramidal type. The dynamics of these latter depend, in the last analysis, on the same hip muscles which control the dynamics of the proximal portions of the legs; the distal dynamics become, however, richly differentiated in biodynamic detail, not when these details are incorporated in the effector impulse and are first reflected in the dynamics of the pliant proximal points, but only when *functional integration of the receptors and effectors* is achieved and when the effector side of the nervous system learns to seize the fleeting moments of functional conductivity.

The reliability of this explanation is well illustrated by observations on the world-famous runner, Jules Ladoumeg. In his case, the dynamic curves of the distal limbs reach their maximum degree of resolution, far exceeding the degree of resolution observable in the curves of other runners; and, further, in his case this degree of resolution was accompanied by a particularly rich set of modulations of forces in the distal limbs corresponding to extremely accurate control of external, biodynamic processes. In the complicated multijointed pendulum, by which the leg may be represented in biodynamic terms, the dynamic interactions of the limbs, the play of reactive forces, the complex oscillations of the links, etc., are extremely varied and abundant; the fact that they are kept in the background in the case of this great runner, but have at the same time such abundant reflections in the dynamic curves, is evidence of the extremely delicate degree of adaptation to proprioceptive signalling achieved by Ladoumeg's neuromotor apparatus. It is precisely this adaptability which allows him a high degree of differentiation and control over the active dynamics of his distal limbs; in his case this is accompanied by a considerable degree of quantitative economy of force.

We may also cite in favour of this explanation an observation made by T. Popova. For a given value of the velocity in running in various children, such of them as have at the time of observation a more differentiated biodynamic structure give as a rule smaller amplitudes of acceleration, that is to say, a smaller range of dynamic forces. In order to arrive at the same final result the child with the qualitatively less differentiated dynamic picture must expend more energy. This can only mean one thing: that a higher degree of resolution of the distal force curves is a sign that the system is learning to seize the moments of least resistance or, to put the matter another way, to utilize the whole rich play of external forces and possibly also the entire physiological (involuntary) gamma reciprocals and other more complex reactive processes at the muscle periphery.

The further development of running in children after the age of 5 closely repeats that for walking and I shall not dwell on it at present.

An analysis of changes in walking in old persons undertaken by P. Spielberg* has reinforced the data discussed above on the *development* of the structure of the locomotor act with interesting data on its *involution*. Spielberg distinguishes three involutional stages in the walking of old people. In the first of these stages some decrease in the normal activity of the structural mechanisms of walking can already be discerned, but this decrease is effectively compensated for by the involvement of the higher psychic functions in the realization of the act of walking: consciousness, voluntary attention, and so on. In the second stage of involution this alerting of conciousness gives way to a heightened degree of fussiness, hyperproduction of movements, hasty and short steps, etc. The inventory of the dynamic structural elements becomes poorer; the vertical wave b_2 for the foot gradually diminishes and then disappears (in early childhood this wave develops, on the other hand, last of all), then the peak of the longitudinal component β undergoes attrition. The reactive wave α is retained longer. In the third stage we observe gross dissolution of the structure of movement. The force curves become small in amplitude and impoverished in terms of their components. They lose element after element. Meanwhile, the equality between successive steps disappears and

* This study was undertaken at the Laboratory of Physiology of Movement of the All-Union Institute of Experimental Medicine.

irregularity begins with alternation of relatively large and small steps and deeper signs of disco-ordination (disorder of the forms of the S curves). To this picture of decay we may also add P. Spielberg's observation of the disintegration of normal unitary co-ordination. The synergy existing in normal walking between the action of the arms and legs is destroyed, the movements of the arms become arrhythmical and the amplitude of these movements gradually diminishes to zero, after which the arms are stretched out rigidly slightly in front of the body—as if in constant readiness to support the body in case of falling. The vertical amplitude at points of the feet is still perceptible, but amplitudes for the upper portions of the body rapidly decline to zero, destroying the normal proportion between movements of the upper and lower portions of the body. In extreme senescence a man eventually has force curves which are as devoid of peaks as his jaws are of teeth. Among the force curves there survive only the earliest reciprocal elements ε and n_a (not counting α) and some vestiges at times of ζ, and at times of γ or η. The dying of the structure is clearly marked in this material.*

In this way the ontogenetic material has shown us beyond all doubt that the biodynamic structure of walking emerges, passes through a series of regular stages of development, and then regularly involutes in senescence. Most important in principle is the fact that this development is related to extremely determinate *qualitative* changes in the structure itself. In respect to its *morphology*, this structure passes in early ontogenesis through: (a) a reciprocal innervationally primative stage; (b) a stage of gradual development of morphological elements; (c) a stage of abundant proliferation of these elements; and (d) a stage of inverse development of infantile elements and the final organization of complete and proportional forms.

In their relations to *motor co-ordination* the biodynamic structures of walking pass through a series of qualitatively different stages of development in exactly the same way.

(1) At the beginning we encounter the signs of general hypofunction of proprioceptive co-ordination. There is no correspondence between positions and dynamic phases; there is no unity of S for the existing adjustment between W and F; there is no similarity of S for various children.

* In recent times, extensive and interesting studies of senile gait have been published by R. Drillis [81].

(2) Later the child passes through a stage of development of proprioceptor co-ordination *post factum* (compensation by means of secondary co-ordination) and only significantly later on develops:

(3) Co-ordination *ante factum,* or more accurately, *in facto* (adjustment or primary co-ordination).

It is perfectly natural to compare these sequences in morphological and functional development. This comparison may give as a key with which to decipher the meaning of particular morphological phenomena.

We may first suppose that the initial ontogenetically earliest (and clearly also phylogenetically the most ancient) impulses ε and the infantile n_a are *spontaneous preproprioceptive impulses.* They represent the original and most ancient framework of movements, their rhythmic and dynamic basis. All the waves developing later, which are brought forth during the period of the development of compensatory co-ordination, are already indubitably effector responses to proprioceptive signals; we have termed these waves *innervationally reactive.* Among these waves we have, for example, ζ and β. The connections between the positions of a moving organ and its velocity must be biodynamically characteristic for these waves.

Finally, the appearance of forms and of concrete proportionalities in the dynamic curves is deeply involved with the development of compensatory co-ordination, that is, with the activity of those highly organized apparatuses of the central nervous system which ensure the completion of the entirety of a projected movement, the definition and accuracy of movements, etc.

And so we have established at least three forms of elements among the component waves of the biodynamic structure which differ from each other in essential ways: (1) *spontaneously innervated,* the earliest and most primary (ε and n_a); (2) *reactively innervated* (γ, ζ, β); and (3) *mechanically reactive* which do not have as their basis either innervational impulses or changes in muscular activity, but which arise entirely at the periphery as a result of the complex collision of internal and external forces in the kinematic linkage of the extremities. Amongst these mechanically reactive waves we may place α, which will be discussed further, and a whole series of other smaller waves.

4. A Sketch of the Qualitative Analysis of the Biodynamic Elements of the Locomotor Act

In the "constellations" of biodynamic elements which we have observed and studied, the degree of visibility and clarity of the individual elements and the degree of investigational interest they possess, are not always coincident. This has been the case in regard to astronomical constellations, where very often objects of the first magnitude, the "alpha" of the constellations, have considerably less scientific interest than some quite faintly discernible phenomena such as "delta" of Cepheus, which not so long ago was epoch-making in astrophysics. However, the large and bright objects are always noticed first and they provide the investigator with an impetus towards the examination of their fainter fellows.

This also occurred in the present study in the case of the first magnitude star of the α wave. At present this wave is of considerably less interest to us than such weak and nebulous objects as the ζ group in walking, or the A' and $n_{\beta 2}$ waves in running, but it originally guided our investigational group towards the study of waves in general. For this reason it deserves a short general characterization.

The tension of the flexor musculature at the knee results in the bending of the lower leg and foot backwards *relative to the knee,* though the movement in space of the knee itself and of the thigh with it, is not predetermined by this. According to the basic principles of biomechanics the musculature at the knee cannot displace the centre of gravity of the leg as a whole either forwards or backwards, but only along the straight line joining it to the hip joint, that is to say, in walking, only upwards or downwards. For this reason the isolated operation of the musculature at the knee moving the lower leg and the foot backwards inevitably moves the thigh forwards in compensation. The same *forward* displacement of the thigh is effected even in a case where it is itself pulled gently *backwards* by the action of the hip musculature, especially because this latter must surmount significantly higher moments of inertia than the musculature at the knee.

In this way the result may be that, should the moment of flexion in the hip muscles be not much greater than the moment of flexion at the knee, there occurs only a very slight backward displacement of the centre of gravity of the leg as a whole, whereas the momentum at the knee can effect considerable flexion of the more compliant

shin-and-foot system relative to the knee. As a result the thigh will be displaced *forward* in spite of the fact that the hip muscles are pulling it backwards. If it were not for this pull the thigh would be
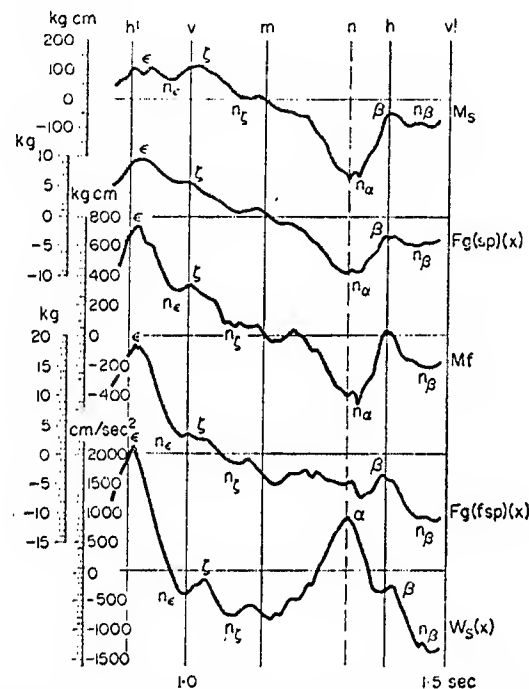

FIG. 29. Curves for the muscle force moments in normal walking compared with curves for the forces and accelerations of the limbs of the legs. From top to bottom: 1, the force moments in the knee joints; 2, the longitudinal components of acceleration at the centre of gravity of the shin–foot system; 3, the force moments in the hip joints; 4, the longitudinal components of the forces at the centre of gravity of the leg as a whole; 5, the longitudinal components of acceleration at the knee joint.

displaced even further forward; for it not to be moved forward at all it would be necessary for the flexing force of the hip muscles to reach a significantly higher level. So towards the end of the swing period, forces which operate *forward* arise in the thigh in spite of the fact that the whole of the surrounding musculature, both at the knee and at the hip joints, is pulling *backwards* at that moment

(Fig. 29). This constitutes the force wave α which we term *reactive-mechanical* for the quite logical reason that it arises in opposition to the muscle forces at a given moment, entirely as a result of the peripheral interplay of action and reaction in the complex kinematic linkage of the leg.

It is clear that if the knee joint were to be immobilized in any way the wave α would rapidly disappear.

This is confirmed in fact. In *Handbuch der normalen und pathologischen Physiologie*[*] is cited a cyclogrametric of the forms of the curves for the longitudinal velocities of the knees in the walk of a subject with strained ligaments at the knee joints. Because of pain in the joints this patient walked carefully avoiding flexing his knee joints (antalgic walking) and as a result there is no sign of the α wave in the curve obtained for his knee (this wave forms a second smaller prominence in the normal velocity curve for the knee (see Fig. 29, on left). We have also tested this position experimentally. A healthy subject had his knee joints splinted and bandaged, and as a result the α wave entirely disappeared from the curves or was at least very much reduced. The latter fact may be explained by some "leakage" of the flexibility of the knee as a result of the bandages not having been tied tightly enough. It is interesting that under all these conditions the β wave which, in normal walking, almost merges with the α wave, and is difficult to distinguish from it with the naked eye on normal curves for the thigh, becomes completely isolated, and begins to tower above the remnants of the α wave. All this gives final and conclusive proof that α is a reactive-mechanical curve. We found an opportunity to put this problem to experimental verification, which now leaves no doubt in the matter.[†] A subject with a very short above-knee amputation had an artificial limb which replaced the lower section of the thigh, the knee joint and the shin and foot. It was possible to lock the knee joint or to give it some passive flexibility restricted on both sides by elastic buffers. When this subject walked with the knee joint locked, as can be seen in the cyclograms, the curves of movement do not show the smallest trace of α; when, however, the lock was left open, the artificial limb

immediately began to reproduce the phenomenon of α in walking (Fig. 30). It would be difficult to prove more completely the essentially mechanical nature of this phenomenon.*

We must at once admit that it appears, on the basis of our most recent observations, that the α phenomenon is not entirely *mechanically reactive*. Some accessory phenomena of an innervationally reactive type begin to be apparent in this wave. The appearance
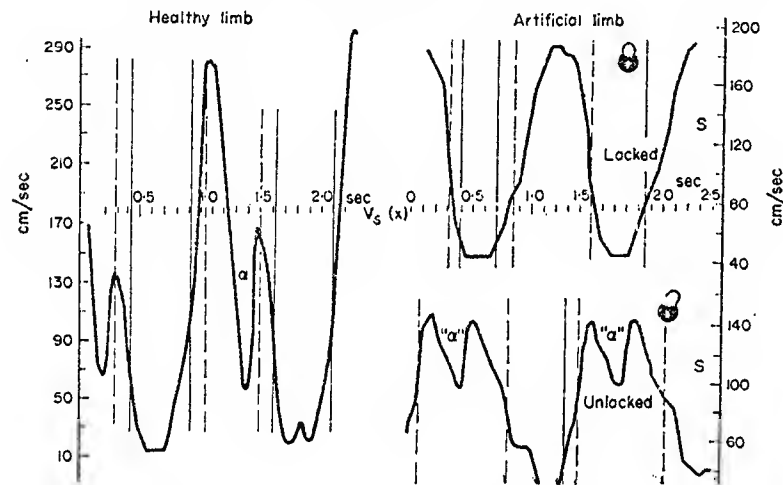

Fig. 30. Appearance of force and reactive wave α at the knee hinge of a prosthesis after unlocking of the hinge (from a study by O. Saltzgeber carried out at the Central Institute for Study of the Disabled).

of α in running is not limited to the single simultaneous pair of waves n_α–α, but gives rise to an entire chain of successive waves. This might be expected as, in life, no phenomenon is exhaustively described by any single explanation.

It is possible to count very many mechanically reactive waves in locomotion and there certainly exist even more mechanically reactive components which are part of phenomena of another type. Among mechanically reactive waves we may enumerate, for example, the childhood ζ which is an echo of the force n_ζ (the beginning of the main reverse wave n_α); the waves n_α and n_φ of the

* The flexing force of the knee muscles necessary for the appearance of the α phenomenon is replaced in this case by the force of the springs in the knee joint of the artificial limb.

Prussian goose-step, and so on. We may include among mechanically reactive components the lowering of the ζ area in the thigh as compared with the centre of gravity of the whole leg in normal walking, indicating the effect of reverse reaction in the thigh as a result of the tension ζ of the extensor muscles of the knee. We may also refer to this category the passive maximum flexion of the knee in running, which occurs in spite of the quite considerable and long-lasting tension of its extensor muscles. By thoroughly studying one representative of such a family we may now quite easily establish its position in the same family of less distinct objects. It is only necessary to formulate common characteristics by which these may be recognized.

The basic indication of mechanically reactive waves is the presence, in the curves expressing linear force or acceleration of a limb, of any waves which are absent in the corresponding moments in the curves of muscle momenta of the nearest proximal joints. This most essential sign answers the question of the mechanically reactive nature of a wave at once and without further argument. To employ here another of the terms popular with morphologists, the curves of momenta are the best reagents for the recognition of elements of this type.

The second indication is less rigorous and less general, but is nevertheless more conveniently used in the majority of cases, as the "momentum reagent" is very time-consuming and therefore expensive. The condition is that the mechanically reactive wave always arises as an offshoot of another active wave, making itself felt in one of the intermediate limb segments. From the explanation of the α wave given above it is apparent that the mechanically reactive wave arises because it is impossible for the internal muscles of a system to displace the centre of gravity of the system. Because of this, if the internal muscles communicate an acceleration to a single link in one direction, another link will undergo compensatory acceleration in the opposite direction in a mechanically reactive manner. The second indication mentioned above follows from this: if, in two adjacent limbs of a freely moving system (for example, in the swing of a leg), there exist two simultaneous waves in opposite directions, it is almost always the case that these are a mechanically reactive pair and that one of the elements represents a reaction of the recoil type.

It goes without saying that a very careful analysis of the surround-

ing phenomena is necessary here in order to recognize which of the two waves of a pair is active and which is reactive, and whether it is possible to regard the phenomenon as being entirely mechanically reactive or whether innervational components are incorporated in it.

The meaning of this analysis is quite clear. It is only after eliminating from the picture of a movement such components as are imposed upon it from the periphery that it is possible to say that it really reflects the internal processes of innervation. Braune and Fischer, in their time, thought that it was possible to go about the matter in the opposite, synthetic way by setting determinate dynamic conditions and attempting to resolve the manner in which the complex, many-linked pendulum of a limb must move under these conditions. The problem is completely unresolvable mathematically if approached in this way because of its extreme difficulty. We have chosen the other approach, which is much easier, and which is in any event always possible. We take the evidence of real live movements which are already established and integrated by nature, and we then gradually free them of all their external mechanical components, that is always possible by analytical methods. After this preparation only the central innervational core of a movement remains and this is appropriate for further purely physiological investigation to reveal how, and in what way, the discrete events occur.

At present we stand only at the very beginning of this study. Much time has been spent on the development of techniques and not a little on the formulation of the questions. Nevertheless, some observations, still difficult to systematize, have already begun to accumulate in directions that reveal the nature of biodynamic elements. Some of these observations I summarize here.

If the curves for the forces in various limbs of the body are examined together, in terms of the same component, then it is at once strikingly obvious that whole series of these elements are common to all limbs. In all the curves for a given moment there occurs, with a greater or lesser degree of synchrony, a distinct direct wave (maximum wave) or a reverse wave (minimum wave). In other cases this generality is not apparent, and sometimes the maximum wave of one limb or system corresponds more or less in time with the minimum wave of another limb or system. We designate waves of the first type as *univocal* (i.e. single-signed), and waves of the

second type as *contravocal* (i.e. opposite-signed). Exceptions are almost unknown to the rule that the *point of the body on one side of which the waves are univocal, and after passage through which they become contravocal, incorporates the active dynamic source of these waves.* If at any given moment all points of the leg located below the knee display greater or lesser synchrony at the maxima of their force curves, while, above the knee, instead of the maximum there appears a minimum in the curves of the same components, this signifies that the dynamic cause of all the waves which have been examined lies in the musculature about the knee. We see an expression of this law both in the case of the reactive pair n_a-α described above and in the case n_r-ζ in the walking of children.

It follows from this observation that if any given wave can be followed in the same form through the entire length of a given limb, the source of arousal of this wave is located outside this limb. In this way we may be sure that the sources of the b_1, b_3, b_4, b_5 waves of the main vertical thrusts in walking lie outside the leg, since they appear as univocal waves in all the force curves of the leg. Moreover, as these waves are univocal for both sides of the body they cannot be referred to the hip musculature of one leg—yet another proof of their high degree of integration.

The same cannot be said of the b_2 wave in the thigh (see Fig. 24), which we see to be in almost exact synchrony with the trough (minimum) n_2 in the curve for the vertical forces in the shin and foot. The change of sign takes place in the region of the knee, which means that the musculature of the knee is somehow involved in the appearance of this pair b_2-n_2 (it can hardly be involved on its own because the case is complicated by the absence of a strict synchrony between b_2 for the thigh and n_2 for the shin and foot).

Clearly, most longitudinal waves in the swing period (other than α) arise outside the leg; in the curves for running it is possible to follow the univocality of the majority of these waves over an interval approximately from δ to ζ with particular clarity. At the same time the origin of these waves is clearly established by the circumstance that the waves simultaneous with them in the other leg are opposite in sign to the former (see Fig. 27(b)); this means that the source of the force lies in the hip musculature—in the region joining one leg to the other.

There are signs which allow us to specify, in many cases, not only the muscular region where a given element appears but also its

deeper innervational properties. We are obliged to consider a number of cases (running, marching, etc.) where the force wave rises and falls in strict parallellism with changes in the angle of articulation; the more strongly, for example, the hip joint is extended, the more intensive becomes the flexion moment in this joint. The maximum of the angular displacement and the maximum of the force or of the moment become almost absolutely synchronous, or the maximum of the force lags by a few milliseconds in relation to the maximum angular displacement. This relationship leaves no doubt of the fact that the given wave is a reflex produced by the extension of a muscle group; a reflex of the myotatic or Eigenreflex type, etc. Similar phenomena are also regularly encountered in running (the n_4 wave), in the goose-step (n_2), and in stepping to three-part time (n_1). Apparently these occur only under conditions of very considerable angular displacement of the limbs from their mean positions.

There are waves which display very little relationship to the degree of angular displacement, but a very close correspondency to position. As we have already said above, in general the majority of dynamic phases in normal healthy walking are very closely related to the specific positions in which they occur. This is an indication that proprioceptive elements are involved in all of them. Some waves are, however, more easily separated from their usual positions by changes in the type of locomotion than are others. So, for example, we may be sure that in the various forms of marching the ζ wave is so indissolubly linked with the positions normal to it in walking that even the usual order of succession of waves is destroyed. Usually, in normal walking ζ begins after the reflection of the front thrust b_1, while in the three-part time marching step ζ occurs earlier than b_1, but at the precise moment when the leg reaches the ζ position. The b_1 wave is displaced by the conditions of the change in gait, but the ζ wave is not.

In running, a wave which corresponds to ζ in all respects begins, however, at another position of the leg than in walking. It is possible that we are not justified in calling this a ζ wave and it is also possible that it is simply the case that there are in general no positions in running that resemble the ζ position for walking, so that the entire kinematics of the transfer of the leg are completely different in the two cases.

This question as to the extent to which it is permissible to apply

to one or another wave the symbol of a wave which has already been investigated in the context of quite another form of locomotion leads on to a very important general question: to what degree are waves which we have designated by the same symbols in various forms of locomotion really homologous and not simply analogous?

This question has been analysed by us primarily in relation to three groups of objects: in walking of children, running and military marching. In all these cases we have come to the conclusion that among the dynamic waves of various forms of locomotion we undoubtedly encounter analogies which have only an external mechanical relationship with each other and gross differences in their nature (for example, the n_2 wave in the Prussian goose-step and the n_1 wave in the triple-time step); however, it is usually not difficult to distinguish these from true homologs. In general, all the data on the course of the development of movements, and a careful analysis of qualitative variations, indicate that the waves to which we have given a single name in all these types of locomotion are real genetic homologs in the overwhelming majority of cases. Nevertheless, the question, for example, of the nature of the integral waves of the vertical components is still sufficiently complicated for us not to be able to establish any homology between running and walking, so that we have given the vertical curve for running a separate nomenclature.

Important material for the determination of internal similarity of different waves may be obtained by observing the chronology of these waves. We have only just begun an analysis of components of this type, but it is necessary to say a few words on the topic at this point. If we study the waves of the curves of various points of the limbs it appears that waves which are absolutely synchronous at all points of the limbs do exist (for example, ε' or n_{B_2} in running), but only as extremely rare exceptions. Any given wave usually runs along the limb from top to bottom, or from bottom to top; some waves pass through these stages faster than others. The classic central spontaneous waves ε and n_a move along the leg from top to bottom—from the centre to the periphery. Waves which are reactive thrusts from external forces spread from the point of application of these forces, for example, the supporting front thrust C in running. It is still difficult to say whether this is absolutely correct.

It is interesting that for a number of waves which have been studied the velocity of the passage along the limb is close to the

velocity of passage of a nerve impulse along a neuron. This raises a series of very interesting problems which will definitely form topics of investigations in the immediate future.

5. Conclusions towards the Study of Motor Co-ordination

It is necessary as a general summary of this chapter to say a few words indicating in what respect the material published here will offer new points of departure for the understanding of motor co-ordination.

The understanding of motor co-ordination, like many other scientific goals, has been achieved by a negative method—through observation of the phenomena of lack of co-ordination—and has been only gradually enriched by the accumulation of observations on pathological movement. Like all knowledge acquired by negative means it has constantly suffered, and suffers at present, from the absence of accurate determinations.

Knowledge about the processes of co-ordination is not obtained deductively from knowledge of the effector process. Until the present, while the moving periphery has been regarded as an exact somatic projection of the central effector apparatus, reproducing in the form of movements with particular exactitude and simplicity all those chains of effector impulses which operate in it, there has seemed no need for any special physiological organization in the form of co-ordination. If the centre transmits a regular and efficient chain of effector impulses to the periphery, it will appear at the periphery in the form of equally regular and efficient movements; if the chain of central effector impulses is irregularly and inefficiently organized, its peripheral projection will also be an irregular and badly organized movement. But in both cases the movements will be *co-ordinated*, that is, they will accurately reflect what is contained in the central impulse. Both of them will be accurately fulfilled (reflected) at the motor periphery, in exactly the same way as a grand piano reflects with equal accuracy the playing of a good or a bad pianist.

Knowledge of co-ordination ought to be applied to the explanation of the effector process only from the moment when it becomes clear that the motor periphery does not have such rigid mechanical connections with the centre as were taken for granted in the pre-

ceding examples. *Movements are not completely determined by effector processes.*

But, if it is inadequate to send to the periphery any completed effector impulse in this way, and it is still necessary to attend to the periphery to ensure that it has obeyed by being moved in the required direction, there must exist together with the initial effector system more or less complicated auxiliary systems which ensure constant and complete *control* of the periphery by the centre. The deeper the functional gap with the absence of univocality between the centre and the periphery, the more complex and unstable is the real relationship between impulses and movements; the greater (in mathematical language) are the number of degrees of freedom of the motor periphery relative to the central effector, the more complex and delicate must be the organizational control to which we have referred. This organizational control is motor co-ordination.

In this context the idea of co-ordination is in the closest relationship to the idea of *functional non-univocality* of the connections between the motor centre and the periphery, between impulses and effects. The more our knowledge of the forms and types of these univocalities increases, the deeper becomes our understanding of the co-ordination of movements.

At present a whole series of sources of this indeterminacy are known. In the first place we must recall the *anatomical* sources described earlier. The fact of the presence of a large number of degrees of freedom of movement at the joints, and more so in the complex kinematic chains found in the make-up of the organism, provides very many conditions for indeterminacy. Among these we may count the impossibility of the existence of fixed anatomical antagonists at many joints; the variation in the function of one and the same muscle group at a multiaxial joint in relation to the disposition of the limb segments; the multiplicity of action of muscles, first described by Fischer, where they act on more than a single joint, and so forth. Amongst anatomical sources we must also mention the fact of multiplicity of innervation of the skeletal muscles, resulting in their convergent motor dependence on a whole series of conduction pathways both in the central and in the autonomic nervous systems.

Next there are a number of sources of indeterminacy of a *mechanical* order such as we attempted to investigate in experimental terms. Among basic facts of principal significance in this respect we must include, first, the fact described above of a closed dependence

between muscle tensions and movements—a fact establishing the presence of indeterminacy in strictly mathematical expressions and directly pointing to the necessity for at least two conditions of integration independent of the primary effector impulse.

The second principal fact in this group is the existence of a high degree of mechanical complexity in the multisegmental kinematic chains (of the limbs and, in particular, of the body as a whole) which conditions the great abundance of all sorts of reactive forces and moments in these chains and makes them extremely capricious and uncertain instruments for the fulfilment of movements. We should note here that the mathematical theory of pendulums with many links is extremely complicated and leads to solutions only for a few particular cases, and that so far we have been quite unable to employ multilinked kinematic chains in which more than a single degree of freedom is used at one time in contemporary technology.

The third group of sources of indeterminacy has begun to be described only during the last 10 or 20 years as new data have been obtained. This is the *physiological* group. In this group we must include all such data as give evidence of selective relationships between the motor periphery and effector impulses reaching it. If in previous years the pathway followed by the effector impulse from the giant pyramidal area of the cortex to the myoneural plates appeared to be (functionally) continuous and uninterrupted, now the matter must be considered in a new light. The selective and integrational character of the function of the synapses at the anterior horns has already been explained by Sherrington. The principle of isochronism of Lapicque may serve as a possible explanation of these phenomena. The observations of Adrian's school on the spinal transforms of rhythms when compared with the abundant material on lability and parabiosis emphasize still more the physiologically active nature of the latter synapses. The selective character of myoneural transmission has been demonstrated by Lapicque and has also been elucidated in an original way in the studies of Paul Weiss. The active filtering role of the motor periphery in respect to the impulses that reach it appears to hold true for all these data, as does the fundamental dependence of this activity not on the central relationships but on the afferentational field.

All these many sources of indeterminacy lead to the same end result; which is that the *motor effect of a central impulse cannot be decided at the centre* but is decided entirely at the periphery: at the

last spinal and myoneural synapse, at the muscle, in the mechanical and anatomical changes of forces in the limb being moved, etc. It is thus obvious that the decisive role in the achievement of motor control must be played by *afferentation* and that it is this which determines the physiological conductivity of the peripheral synapses and which guides the brain centres in terms of the mechanical and physiological conditions of the motor apparatus. The central effectors achieve co-ordination of movements only by plastically reacting to the totality of the signals from the afferent field, adapting the impulses transmitted to the situation that actually obtains at the periphery.

Co-ordination is therefore a type of complex sensory motor reflex beginning with afferent input and ending with an exactly adequate central answer. The afferentational input part of this reflex is, however, itself a form of reaction of the periphery of the body to the beginning or course of a movement. We observe in this phenomenon a sort of inverted reflex where the effector pathway acts as the exciting arc and the afferent nerve pathway acts as the reacting arc. The point of closure of this reflex arc appears here as the functional connection between motor impulses and the resulting movements, i.e. the same area of physiological indeterminacy which was discussed above. For this reason this functional area deserves a metaphorical description as a peripheral synapse.

Because this is so we may guess that the structure of the co-ordinational reflex differs considerably in principle from the sensory reflexes known to us from other areas; the co-ordinational reflex is not an arc *but a closed circle with functional synapses at both ends of the arcs.* In this reflex the centripetal impulses as in all other reflexes are transformed above into centrifugal ones, but the centrifugal impulses going out to the periphery are there rapidly converted into new centripetal impulses.

Like every other form of nervous activity which is structured to meet particular situations, motor co-ordination develops slowly as a result of experiment and exercise. Since co-ordination is, as we have established, a means of overcoming peripheral indeterminacy, it is clear that the basic difficulties for co-ordination consist precisely in the extreme abundance of degrees of freedom, with which the centre is not at first in a position to deal. And, in reality, we observe as a rule that improvement in co-ordination is achieved by utilizing all possible roundabout methods in order to reduce the

number of degrees of freedom at the periphery to a minimum. When someone who is a novice at a sport, at playing a musical instrument or at an industrial process first attempts to master the new co-ordination, he is rigidly, spastically fixed and holds the limb involved, or even his whole body, in such a way as to reduce the number of kinematic degrees of freedom which he is required to control. Invertebrate organisms have in their make-up a form of co-ordinational surrogate in mechanisms of muscular locking *(Sperrung)* which by physiological means eliminate such degrees of freedom as are unnecessary at any given moment. But we must add that all lower forms of vertebrates (up to birds inclusively), for which the striatum still predominates over the cortical hemispheres, possess analogous auxiliary muscular mechanisms and employ them widely. Lizards, snakes, many brooding birds (eagles, parrots, etc.) are as rigid as statues in the intervals between voluntary movements. Reptiles show particularly clearly a statue-like stiffening of the body as soon as successive voluntary movements cease. If a lizard turns head to tail its body and limbs are motionless as sculpture. Mammals, apparently in healthy condition, find similar locking completely superfluous, and return to it only in cases of diseased hyperfunction of the extrapyramidal system (catalepsia, catatonia, hypertonic symptom complexes in encephalitis). In the norm there is no rest in mammals and in human beings, and outside of deep sleep there is no similar immobility; careful observation of standing or sitting human beings, dogs or cats give evidence of this. Even the set immobility of a cat or a tiger is quite unlike the immobile period in a reptile (or a spider)—it is sufficient to watch its tail.

Artificial tetanic elimination of superfluous degrees of freedom which is observed in the form of tenseness and constraint gradually gives way during the course of training to complete freedom. Having mastered the first degrees of freedom the organism increasingly raises its ban on further degrees of freedom. Where there has been a high degree of expensive tetanic fixation, now there comes a greater economy of movement and a diminution of fatigue. Here two successive stages of release may be observed. The first degree corresponds to the lifting of all restrictions, that is, to the incorporation of all possible degrees of freedom. They no longer interfere with the movements of the organism but introduce complicating reactive phenomena, additional oscillatory frequencies, and so on. The organism has learnt to extinguish them, not prophylactically

(by eliminating the given degree of freedom as a whole), but in an innervationally reactive way (by means of single dynamic impulses). The second, highest stage of co-ordinational freedom corresponds to a degree of co-ordination at which the organism is not only unafraid of reactive phenomena in a system with many degrees of freedom, but is able to structure its movements so as to *utilize entirely the reactive phenomena* which arise. Our material allowed us to examine a great many such cases, both in great masters of movement and in advanced students of movement.

Apparently this second stage corresponds to that described by sportsmen and music teachers as "relaxing", a phenomenon which they instinctively feel but which they do not know how to describe. The economical effect of the transition to this stage is apparent; not only is there evidence here of minimal use of physio-reactive-innervational impulses, but it is also the case that all those mechanical-reactive forces in the complicated link systems, which, in the best cases, occurred without damage at the previous level of co-ordination, are used in a positive sense. This second co-ordinational level is a biological control of highest perfection which explains the great wealth of kinematic utility of the degrees of freedom in the higher mammals—evidence that a level of co-ordination is possible at which this wealth is of immediate use.

It is much more difficult to determine the means by which the organism so far overcomes the internal physiological indeterminacy of the periphery; it is, however, perhaps possible to make a few suggestions at this point.

All that has been said above on the initial suppression and later use of the multiplicity of degrees of freedom may be put in the following way. The movable limbs of the organism do always respond in the same manner to the impulse which is transmitted through the muscles. The secret of co-ordination lies not only in not wasting superfluous force on extinguishing reactive phenomena but, on the contrary, in employing the latter in such a way as to employ active muscle forces only in the capacity of complementary forces. In this case the same movement (in the final analysis) demands less expenditure of active force. It is possible to express this (by means of an analogy with simpler, but similar, electrical phenomena) in the form of a statement that in the second case the reactive resistance of the moving system to the neuromuscular impulses is less than in the former, or, which amounts to the same thing, that its reactive

conductivity is higher in the second case than it is in the first. A higher degree of co-ordination secures a higher reactive conductivity to muscle force impulses at the periphery. We must note that, because this heightening of conductivity is entirely achieved by employing the *dynamic* transitory phenomena, such high conductivity cannot be a stable or constant value. The mastery of co-ordination must consist in the ability to give *the necessary impulse at the necessary moment*, seizing the fleeting phases of higher conductivity of force and avoiding those phases during which this conductivity falls to low values.

It is quite in order to draw an analogy here between the examples of reactive-mechanical conductivity which we have studied and those phenomena of changes in synaptic conductivity, mentioned above, which have been explained by neurophysiology in recent years. Observations both by Lapicque and by P. Weiss indicate that the effector impulse *may arrive but not pass through*. It is obvious that at this level also the most effective impulse will be that which arrives at a synapse at the moment of its attainment of a level of highest conductivity, or that which is, by its nature, most adequate to meet the conditions of conductivity (lability) at the final synapse (which from the point of view of the result amounts to the same thing). It follows that in this case also co-ordination will consist in the ability to order events so that the effector impulses will encounter conditions of the greatest physiological conductivity at the periphery and will not collide with phases of physiological refractoriness which would doom them to ineffectuality.

The role of co-ordination at this level must therefore consist in the *preparatory organization of the motor periphery in order to guarantee optimal selection of conductivity*. This opinion is extremely unusual but necessarily proceeds from the facts. As the effector impulse cannot in principle bring about by itself a co-ordination without being entirely dependent on afferent processes, we must not regard this impulse as somehow precisely differentiated—as there is no biological basis for this. There is no possibility that accurate *effector* differentiation can be developing here because, as has been shown above, the peripheral indeterminacy demands different effector connections for each successive repetition of a given movement. Co-ordination at the level described lies basically not in the character and the accuracy of a tetanic effector impulse but in the accuracy of some sort of preparatory (not tetanic) effector

impulses *which organize and prepare the periphery* for the reception of the right impulse at the right moment. The co-ordinational process does not enter into the composition of the tetanic impulse, or follow immediately after it; it goes *before*, clearing and organizing the path for it, and therefore must operate through quite different paths and employ quite different innervational processes.

What may be the path along which the co-ordinational process reaches this given level and what are the non-tetanic effector channels which it employs we may at the moment only guess. Nevertheless, it is possible to put forward a few hypotheses in this area.

Firstly, there is no doubt that the co-ordination is certainly not organized independently at the periphery alone and that the preparation of the periphery for the selective transmission of "the right impulse at the right time" discussed above is, to a very considerable degree, centrally determined (in Lapicque's order of "subordination" in its broader sense) by means of a proprioceptive ordination on the level described is reflex cycle. The co-ordinational process on the level described is obviously not a tetanic process, but it undoubtedly incorporates both receptor and effector components.

We find it very tempting to draw upon the concepts of *tonus* to explain the phenomenon described here.

The physiological data available on tonus has considerably extended the initial ideas on this topic which incorporated first only the idea of a condition of elasticity of the muscle fibres. Without any more accurate determinations tonus, in the vocabulary of physiologists, began gradually to cover a very wide range of facts beginning with decerebrate rigidity and extending to Magnus and de Klein's tonus which has already been understood as a very generalized state of the motor periphery of preparation (in particular of the musculature of the neck and body) for the accomplishment of positions or movements.

The older, static concept of tonus as physiological elasticity constricted and retarded the understanding of these phenomena. It seems that there is at present evidence enough to decide upon a judgement, perhaps preliminary, and to say the following about tonus.

(a) Tonus as an ongoing physiological adaptation and organization of the periphery is *not a condition of elasticity but a condition of readiness*.

(b) Tonus is not merely a condition of the muscles but of the

entire neuromuscular apparatus, including at least the final spinal synapse and the final common pathway.

(c) Tonus, from this point of view, is related to co-ordination as a state is to an action or as a precondition is to an effect.

If taken as working hypotheses these suppositions allow us to explain much more.

Firstly, one is struck by the fact (which was not considered before, but which after these hypotheses are made becomes quite obvious) that not a *single case* of pathological co-ordination is known in which there is not at the same time a pathology of tonus, and that not a single central nervous apparatus is known which is related to one of these functions without being related to the other. The cerebellum has for some time been known as an apparatus which is of decisive importance for co-ordination, and it is also the most important effector for tonus. The same is true of the pallidum and the nucleus ruber. Disorders of the vestibular apparatus lead to functional lack of co-ordination and to destruction of tonus. Section of the posterior spinal tracts results simultaneously in ataxia and atomia; both of these are the basic motor symptoms of tabes. Experimental deafferentation rapidly results in the disappearance of co-ordination and the disappearance of tonus. The number of examples of this type could easily be extended *ad infinitum*.

Secondly, we now see the significance of the flexible and reactive tonic reactions studied by the school of Magnus, which were, however, studied because of inadequacies of techniques, mostly in the static supporting organs of the body—the neck and trunk. It is clear that these systemic reflexes of high degrees of plasticity are decisive co-ordinational prerequisites to movement or positions and that their physiologic purpose is not limited to the communication of a necessary and simultaneous rigidity to the trunk of the body but incorporates the entire preparatory reaction of the periphery to the conditions of the external (static and dynamic) field of forces.

Thirdly, tonus and those centrally directed mechanisms which regulate the conductivity of the distal synapses is very clearly explained by the circumstance that the anatomical substrate both of Rademacher's tonical phenomena and of Lapicque's subordination phenomena are one and the same—that is, the lower stage of the extrapyramidal system and the nucleus ruber group. Section of the brain stem at this level gives a picture of a disorganization of subordination—of the return of muscular chronaxie to its constitutional

value. It also leads to a picture of decerebrate rigidity, that is to say a picture of set, non-reactive spread of tonus, with marked appearance of flexion in some cases and extension in others. This correspondence is certainly not accidental and allows us to discuss the position of the anatomical substrate of the co-ordinational layer, referring it to the nucleus ruber group and to the paleocerebellum functionally related to it.

The innervational paths for the control of tonus in our model would be the rubrospinal and the vestibulospinal tracts for the tonomotor effects, and the sympathetic tract for tonotropic impulses.

CHAPTER IV

SOME EMERGENT PROBLEMS OF THE REGULATION OF MOTOR ACTS

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THE period of struggle towards the recognition of the biological importance, the reality and the generality of the principle of cyclical regulation of life processes is now behind us. As often happens during periods of scientific quarrying, glimpses of the new ideas and general forecasts may now be noted in the work of the older classical physiologists (Bell, Sechenov, Jackson), and of those nearer to our own epoch (Ukhtomskii, Wagner). The present author gave an account of the application of these concepts to the problem of the co-ordination of movements in a report in 1929 in which this principle was given a general mechanical foundation [15], and in 1935 he reduced it in general terms to differential equations (sec Chapter II). The debate, in these initial stages, was conducted sharply, but now seems to be over. Now we are living through a period of the extensive development of this principle and of its elaboration and cultivation in heuristic models and in automatic processes in the most varied fields of practical application. Clearly, now is the time to look forward, to attempt to formulate some of the new problems which occur in this area, and to direct attention to some insufficiently illuminated and evaluated aspects to the circular principle of control. The most suitable data to be discussed are from the area of the physiology of motor acts.

I

The motor activity of organisms is of enormous biological significance—it is practically the only way in which the organism not only interacts with the surrounding environment, but also actively operates on this environment, altering it with respect to particular results. The theoretical lag observed in this area in comparison

with the physiology of receptors or of internal processes is therefore very puzzling. So is the neglect which is obvious from the sections on movement in physiological textbooks which vary up to now from zero to some few pages. It is necessary to indicate briefly how great is the resulting loss sustained by physiology as a whole.

If movements are classified from the point of view of their biological significance to the organism making them, it is clear that on the first level of significance we have acts which solve one or another particular *motor problem* which the organism encounters. Leaving the analysis of this expression aside for the moment, we may note that *meaningful* problems which can be solved by motor action arise, as a rule, out of the external environment. This at once draws a distinction between meaningful actions and the range of independent movements which are not concerned with overcoming external forces, or a large number of momentary single-phased movements such as withdrawal of the paws. It is already apparent from this that laboratory physiology which, with very minor exceptions excludes from the experimental chamber all movements except reflexes to pain, defensive reflexes (primarily the scratching reflex*), diminishes its resources of explanation not only quantitatively but also qualitatively, and as we now see not only in relation to narrowly motor problems.

First, if in the ease of relatively independent movements (pointing, drawing lines in the air, etc.), some knowledge in mechanics and biomechanics is necessary in order to demonstrate the incontrovertible necessity for circular sensory regulation, for acts of movement which are concerned with the surmounting of *external forces* this necessity is evident from the outset. In all sorts of motor problems in locomotion (especially complicated ones—running over uneven ground, jumping on to an elevation, swimming through waves, and many other examples), in fighting with other animals, in industrial processes carried on by human beings, the overcoming of *independent* forces is always a prerequisite for solution. These forces are consequently not foreseeable, and because of this they cannot be overcome by any sort of stereotyped movements directed solely from within. A careless consideration of these processes of active interaction with independent surroundings (apparently the

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* The reaction designated as orientation reflex has only been included in this category for terminological reasons, and as far as we know has never been employed for the direct investigation of reflex action.

limitation of explanation to "atomic movements" alone seemed quite justified to the atomist-mechanists of the last century, who regarded a whole as the sum of its parts and nothing more) led to the situation that the principles of sensory-feedback connections, which could have been examined and established for the case of motor control a hundred years ago, remained obscure until the present.

For many years the concept of the open reflex *arc* has been a universal guiding principle in physiology. We cannot exclude the possibility that in such elementary processes as the salivation reflex, or in such abrupt actions of secondary biological significance as withdrawal from a painful stimulus, etc., the arc really does not form *a reflex ring* characteristic for the scheme of the control process, partly because of the short duration of the act, and partly because of its extreme simplicity. However, it is both possible and probable that because of these characteristics of brief duration and extreme simplicity the cyclical nature even of these processes has so far escaped attention and record. (For the process of salivation this is already almost beyond doubt.) However this may be, it seems very likely that a reflex visualized on the model of an *arc* is only a rudiment, or a very special case, of a physiological reaction.*

It remains to describe yet another loss which physiology has sustained from the replacement of real acts of movement solving objective problems as they arise, by fragments of movements of an almost artificial character. This particular loss has so far not been sufficiently emphasized; it has not merely impoverished our knowledge in the area of *receptor* physiology, but contains the root of important methodological errors.

It must be noted that in the detection of *releaser signals* which are incorporated in the operation of one or another reflex arc—the only role in which they were studied by physiologists of classical schools—the afferent systems, at least in the higher animals and in man, function in essentially and qualitatively different ways than in the role of tracking and corrective mechanisms which they play in the fulfilment of motor acts. This difference becomes clear if, once again considering the matter from the point of view of biological significance, we turn our attention to those properties in the receptor organs which had to be developed by natural selection. In

* I would not even exclude the possibility that the first reflex in the form of an arc appeared in the world in the same place as the first "elementary sensation"— both of them in a laboratory experiment, or in the minds of experimenters.

order to act as a *signal-releasing system* the receptor must necessarily have a high degree of sensitivity, that is thresholds which are as low as possible, both for the detection of the absolute strength of a signal, and for discrimination between signals. The most significant biologically are the *distance receptors*, smell, hearing (even of ultra-high frequencies) and vision in various orders of rank for various types of animals. In order to discriminate meaningful signals further from the chaotic background of "noise" it is necessary to develop an entirely analytic or *analysational* function for the corresponding apparatus in the central nervous system. (It is quite natural that I. P. Pavlov, in greatly extending our knowledge of the *signal-releasing* functions of the receptors, should have termed them *analysers* only in his latest years complementing this with the term synthesis.) Finally, the most important mechanism in this signal-releasing role, as Sechenov hypothesized in advance, has been clearly revealed experimentally by investigators abroad (who were stimulated by the practical problems of observation in war) to be the processes of active systematic *search* ("scanning") or examination by telereceptors of every diapason of function. This is an entirely active process, and the effector side of the organism is here employed in a manner completely analogous to that which is later explained to underlie afferentation in the control of movements. I must, however, note at once that this last process has nothing in common with the processes of the evocation of organized effector acts for the integral active perception of objects in the external world, as we shall discuss later.

Once a meaningful motor act has been set in motion by any given sensory signal, the demands of biological expediency on the afferent function are quite different. It was these demands which led to the formation of the processes of annular *sensory correction* during phylogenesis. We may consider the formulation of the motor problem, and the perception of the object in the external world with which it is concerned as having their necessary prerequisites in *maximally full and objective* perception both of the object and of each successive phase and detail of the corresponding movement which is directed towards the solution of the particular problem. The first attribute of the receptors which may be described in the context of this role is that of completeness, or synthesis. This has been adequately described and studied by both psychologists and neurophysiologists under the headings of sensory synthesis or the sen-

sory fields. Among these fields we have, for instance, the body
scheme, the spatio-motor field, the synthesis of objective or quali-
tative (topological) space and so on. The author has attempted to
give a thorough account of the roles of these fields in a book on the
structure of movements [23]. It is here only necessary to recall that:
(1) in this functional area the synthesization of the operation of the
receptors is not manifest theoretically (as was the case above) but
can be directly followed in the norm and in pathology and (2) for
each of such sensory syntheses effecting the sequential direction of
motor acts, the structural scheme of connections between the activ-
ities of various proprio- tango- and telereceptors has its own
specific quantitative and qualitative properties.

In this case the confluence of elementary information flowing
from the peripheral receptors to the central synthesizing apparatus
is so deep and stable that it is in general practically impossible to
distinguish by introspection. All, or almost all, types of receptors
take part in the activity described above (possibly with the excep-
tion of taste alone), but to significantly different degrees. On
the first level there is the general system of the proprioceptors in the
narrow sense; further there is the co-function of all tango- and
telereceptors, organized on the basis of all previous practical at-
tempts in order to fulfil the role of functional proprioception.
Other purely physiological aspects of the operation of the receptors
in the circular function—parameters of adaptation, "comparison
thresholds", periodicity of function, etc.—will be discussed in the
second part of this chapter.

The second determining sign of the receptors as participants
in the annular co-ordinational process—*objectivity*—is of such
great significance that it will be necessary to deal with it more
thoroughly.

It has been possible to analyse receptors in terms of an open
arc only in their role as signals (releasers or inhibitors). It was this
role which led to the use of the term *signal system* for the entire
complex of organs of perception in the central nervous system.
Where perceptual organs operate in this way, objective accurate
information is not, in general, required of afferent function.

The reflex system will operate adequately if to each answering
effector there is attached its own (a) constant and (b) correctly re-
cognized releaser signal-code. The composition of this code may be
entirely arbitrary, without introducing interference into the func-

tional system if these two conditions alone are observed. This
indifference on the part of the central nervous system to the meaning-
ful content of a signal is not a strange, purely biological phenome-
non but part of the very nature of the process of signal apprehen-
sion. This is shown by the conduction of signals, with perfect con-
trol of the necessary connecting and switching in remote-control
apparatus. It is possible to construct two identical automata—air-
craft-projectiles, motorboats, etc.—with identical motors, wheels,
schemes and radio relays, etc., and to organize the situation with-
out any structural differences so that in answer to the radio codes
A, B, C, D, etc., the first system responds with the reactions *1, 2, 3, 4,*
and the second with the reactions *4, 2, 1, 3*, or whatever is wanted.

The characteristics of operation of the receptor system are quite
different, in respect of its control-co-ordinational functioning, in
the process of solution of a motor problem. Here the degree of
objective reality of the information is a decisive prerequisite for the
success or failure of the action to be performed. During the entire
course of phylogenesis of living organisms natural selection in-
exorably sifted out those individuals in which the receptors con-
trolling motor activity operated like a curved mirror. Over the
course of ontogenesis each encounter of a particular individual
with the surrounding environment, with conditions requiring the
solution of a motor problem, results in a development (sometimes
a very valuable one), in its nervous system of increasingly reliable
and accurate *objective representations* of the external world, both
in terms of the perception and comprehension involved in meeting
the situation, and in terms of projecting and controlling the realiza-
tion of the movements adequate to this situation. Each meaningful
motor directive demands not an arbitrarily coded, but an objective,
quantitatively and qualitatively reliable representation of the sur-
rounding environment in the brain. Such an action is also an active
implement for the correct cognition of the surrounding world. The
achievement or failure of a solution to every active motor problem
encountered during life leads to a progressive filtering and cross-
indexing of the evidence in the sensory syntheses mentioned above
and in their components.* This also leads to knowledge through

* The indubitable fact of the existence in the human central nervous system
of *some* qualitatively different sensory syntheses does not contradict the point
made on the objectivity of the representation in the brain. The latter finds an
adequate explanation in the physiology of the co-ordination of movements.

action and *revision through practice* which is the cornerstone of the entire dialectical-materialistic theory of knowledge, and in the cases selected here serves as a sort of biological context for Lenin's theory of reflection.*

The comparison made in the last few pages between the two types of theory of functioning of perceptual systems of the organism which are as yet unequal in terms of their scientific pedigrees and in the extent to which they have been worked out, allows us to illuminate some new aspects of the mechanism of operation of classic signal processes of elicitation, or of differential inhibition, of the reflex reaction.

A long time before telemechanics confirmed the essential principal of *conditionality*† of releasing or switching codes, the same fact was established for biological material by the famous discovery of I.P.Pavlov. The fact that any perceptible stimulus may equally easily be converted into a releaser signal for one or another organic reflex appears to be remarkably universal in biological material. As subsequent studies by Pavlov's school have shown (Speranskii, Bykov), in the entire complex of physiological function, apparently down to the deepest least accessible processes such as hormonal processes or the processes of cell metabolism, there is no single process which may not be connected, and in principle by the same method, to any releaser stimulus. This remarkable indifference of the nervous system to the nature and content of releaser stimuli was noted by I.P.Pavlov at the very beginning of his investigations into the range of phenomena which he discovered. Even the term employed for the stimuli which he grafted on to the trunks of the older organic reflexes—*conditioned* reflexes—is evidence of this. The terminology suggested by V.M.Bekhterev, "combinational" stimuli and reflexes, is less deep in relation to the inter-

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* "Domination over nature appearing in human practice is the result of objectively accurate representation in the head of the human being of the phenomena and processes of nature and this is evidence of the fact that this reflection (within the limits which practice demonstrates for us) is objective, absolute eternal truth." V.I.Lenin, *Materialism and Empiriocriticism.*

† Conditionality in the plan under discussion does not *demand* objectivity and does not contradict it. The comparison and delimitation of the signal-releaser and corrective functions of the receptors undertaken in this paper is probably sharper and more "either/or" than is the case in physiological reality where, doubtless, both forms of function may be superimposed upon each other from time to time and may interpenetrate.

nal significance of the phenomena, but is nevertheless quite adequate to describe the system of such mechanisms as have been explained up to the present time.

Two conditions are always necessary for the conversion of any given supraliminal agent into a conditioned releasing stimulus for any given organic reflex; (1) the coincidence or combination of this agent with the realization of the given reflex within the limits of a short time interval and (2)—an auxiliary condition—a given number of repetitions of this conjunction. The former of these conditions directly relates the phenomenon selected to the *cycle of association by contiguity*, as it were, characterized by an indifference to the meaningful content of the associated items or receptions. It is interesting to note that for the conversion of indifferent stimuli into conditioned releasers their juxtaposition with the *effector* and not with the *afferent* component of the natural reflex is necessary. This last component is employed in the typical conditioning experiment only as a means of establishing and working out the effector arc. This is proved, for example, by the existence of so-called conditioned reflexes of the second order, when the indifferent stimulus possesses releaser properties for a given reflex in spite of the fact that the effector part of the latter is set into action, not by an unconditioned but by a conditioned stimulus of the first order, which was earlier worked into the reflex. Another proof of the above may be seen in the fact that in the methods employed in animal training the reward which reinforces the unconditioned afferent impulses of feeding in the animal is given *after* the correct performance of the required activity in response to the corresponding conditioned command and is not, in this case, the unconditioned releaser stimulus for the trained activity. This detail, which has been underestimated in the past, attracts our attention in the present context because it seems that the formation of associative links in the brain between *afferent processes* and the *effector* portion of the reflex can be explained only if this effector realization of the reflex is reflected (again by means of ring feedback) in advance in the central nervous system, and can there already undergo association with the afferent processes of conditioned stimulation. We may find here yet another confirmation of the fact that "return-afferent" or feedback acts exist as direct components of the process in classical reflex arcs, and only escape observation for the time being.

The second condition of formation of conditioned connections is that termed auxiliary above. It would indeed be difficult to explain why a given number of repeated associations is required otherwise than because of the necessity for the experimental subject to discriminate the new reception introduced from the whole chaos of external stimulation bombarding him. The number of repetitions must be adequate to determine the *non-randomness* of the juxtaposition in time of the intero- or proprioception of the realized reflex with just one particular element out of the totality of extero-reception. In this sense—in relation to the necessary and sufficient number of repetitions—a stimulus which is indifferent in terms of its meaningful content may prove more difficult to discriminate and require more trials if it fails to attract the interest and attention ("orientational reaction") of the subject. The older, naively materialistic conception of gradually "beaten" tracks or synaptic barriers in the central nervous system may already be considered to be relegated to the archives of science.*

We must here mention a fact which remains obscure even in the light of new thinking in the physiology of regulation. The structure of almost all conditioned associations which have been set up is such that a new *conditioned afferent* signal is grafted on to an organic *unconditioned effector* arc. The variation, both in unconditioned effector processes and in the afferent "call signs" which may be attached to them is almost infinite; but almost no single case is known in which we observe the *reverse* structure of a conditioned link, where a new conditioned reflex termination is attached to an unconditioned afferent arc. Cases of this reverse type were to some extent observed in the work of Eroofeeva at the beginning of this century, but I. P. Pavlov himself, in his "Lectures on the Operation of the Major Hemispheres", accompanied their description with a whole series of limitations and reservations. However this structural paradox may be explained in the future, it is clear that the inertia of actually existing effector semi-arcs makes

* If any given indifferent reception is repeatedly coincident in time with some unconditioned process, for example interoreception of salivation, etc., then the so-called probability *a posteriori* that this coincidence is not accidental rises very rapidly, and after ten associations is already very little different from unity. For the formation of a connection it is, however, necessary that both the indifferent stimulus itself, and the fact of the constant coincidence of both stimuli attract attention, that is to say, stimulate the processes of the active reception by the subject.

it extremely difficult to employ their structural mechanism for the learning of unknown movements, for the establishment and learning of habits of movement and new skills, etc.

An examination of the question of signal codes and their conjoint roles in the aspect of regulatory physiology may, it seems to us, throw a new light on the problem of the so-called *second signal system* (I. P. Pavlov). It is clear from the above analysis that the variability in possible conditioned signal codes is not in any way restricted, and that even speech phonemes, which do not in any way illustrate *in this respect* their role as members of any particular class, require, like all signal stimuli, only to be perceived and distinguished from each other.

Nobody has applied the concepts of a second signal system, or of architectonic fields homologous to Wernicke's field in man, to dogs, bears, sea-lions or cats; though all these animals may be trained to set up linkages and differentiations in response to verbal signals (though they are not even all higher mammals), as readily as to other forms of stimulation. These phonemic signal codes, which are not in any way different from other forms of codes, might have been the genetic embryos of phoneme signs in primitive man—a type of rudimentary imperative from which verb forms gradually evolved.*

On the other hand, the *denominational* elements in speech out of which human beings have formed the category of proper names never had, and logically never could have a signal function in the sense described above. For this reason the treatment of the second signal system as a system of verbal representation of *things* (in general, the primary receptions of external objects representing in this sense the aggregate of the elements of the first signal system), which presents itself clearly in the list of names employed by experimenters using the so-called speech-movement method, is the result of a deep and mistaken confusion between two sharply distinct physiological functions and speech categories. *Words as signals* do not form any special type of system, and in the role of releaser

* I must here make the following points: firstly, I do not include in the above any attempt to define the *chronological order* in which verbs and nominative categories may have evolved in primitive man, and secondly, that I agree entirely with well known philologists as to the phenomenon of the *secondary* employment of nominative elements with an exhortatory signal meaning in primitive speech.

phonemes are quite accessible to many animals which are still very far indeed from the function of speech. *Words and speech as reflections of the external world* in their static (proper names) and dynamic action and interaction with the subject (verbs, judgements) do indeed form a system which is attainable by, and characteristic of man alone; but to call *speech* which has attained this degree of meaningfulness and development a *signal system* is to confuse it with one of its most inessential and rudimentary manifestations.*

The idea of a second signal system is doubtless one of the consequences of the methodological confusions described above, and due to the fact that physiologists recognized only one signal-releaser role of the receptor apparatus and undervalued its most important biological and social functions, that is, the cognition of the surrounding world through action and the regalution of action within it. The sign of equality placed between the ideas of reception and signal obliged the investigators of this earlier period to refer even perceived words to the category of signals; meanwhile, it has not been possible to circumvent the striking independence of speech as a specific inherent form of *homo sapien's* symbolic representation of the perceptual world and of himself in it. The tolerance extended to atomism, as mentioned above, has allowed easy bypassing of the *structuring* of speech (which makes it not a collection of words, but an instrument of thought) and its treatment as a sum of speech signals mainly concrete-objective in content.

Russian physiology contrived to avoid another, much more important, gnosiological error perpetrated by many thinkers in the Western world. This is also entirely a result of considering only a single aspect of receptor function: from the fact that it is clearly possible to reconcile the perfect operation of reflex functions with the complete arbitrariness of their sensory codes it is very easy to slide from the position of the recognition of the symbolic nature of all reception in general, and of the conditionality of the picture of the world in the brain and the psyche, to the concept of the

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* We must add to the above that the construction of robot automata which are able to *understand* speech is a quite hopeless problem for modern technology. On the other hand, robots which can react differentially to a few different speech phoneme signs which are given to them may already be built without any difficulty in principle.

un-knowability of objective reality and similar idealistic conceptions which have been disproved by authentic science long ago.

II

We may now attempt to make our analysis of the mechanisms of motor co-ordination in the higher organisms more precise having two problems in view: (1) to extract from this analysis the maximum information available at the present time as to the general laws governing mechanisms of control; and (2) to attempt to discover what constitutes those motor peculiarities of the higher animals, and of man in particular, which sharply and quantitatively distinguish their operation and resources from all that we might expect from the techniques of automatic processes of the present day, and perhaps of the near future. In the present analysis we shall have to touch upon many points which have already been thoroughly analysed in their time [23, 29]; in order to avoid irrelevant repetition I shall dwell on them as briefly as possible in the present report, merely pointing out logical lines of analysis, leaving the reader interested in a more detailed exposition to turn to the works referred to. It will here be best to attempt to complete and extend the questions we have touched upon, which mainly concern the basic principal mechanisms of co-ordination and control, touching in the process upon errors which have now become apparent.

The first clear biomechanical distinction between the motor apparatus in man and the higher animals and any artificial self-controlling devices, as I have repeatedly emphasized, lies in the enormous number (which often reaches three figures) of *degrees of freedom* which it can attain, both in respect to the kinematics of the multiple linkages of its freely jointed kinematic chains, and to the elasticity due to the resilience of their connections—the muscles. Because of this there is no direct relationship between the degree of activity of muscles, their tensions, their lengths, or the speed of change in length. To explain how the control of a movement is complicated by each additional degree of freedom we give the following two examples.

A ship on the surface of the sea has three degrees of freedom (if we ignore rocking movements) though, in practice, control of *one* degree of freedom only—that of the direction or *course*—is enough,

as on the surface of the sea, if the ship deviates somewhat from its course it is not necessary to return to the old *track* in order to establish its former direction, but quite sufficient to follow a path parallel to it, a couple of cables to one side or the other. This problem is easily and adequately solved by an autopilot with a compass. Let us now, however, consider an automobile which must travel along a *road of limited width* automatically dealing with all the curves and bends which it encounters. Here the direction of the car depends in practice upon *two degrees of freedom* of the car's mobility. This analysis shows that irrespective of the means by which the machine receives information on the course of the road (relative, for example, to the centre line), whether this is perceived by photo-, electro- or mechanicoreceptors, etc., the block diagram of the apparatus which guides the car along a winding road keeping it close to the centre line must incorporate: (1) a receptor of the distance from the line, and its sign; (2) a receptor of the angle between the axis of the machine and the line, and its sign; (3) a receptor of the effective curvature of the road; (4) a summing and analysing comparator system; and (5) a system of regulation to suppress incidental swing of the machine to one or the other side of the course. This great increase in complexity is a result of the problem of automatization with only one more degree of freedom. As far as we know no automat of a similar type has yet been constructed anywhere. It is useful to point out that the enormous difficulties of construction are not in any way connected to problems of signalling or to the construction of receptors of the types mentioned; the technical knowledge for receptors of all these types exists at present. The point of the difficulty lies in the organization of the *central recording* of information originally obtained from photo-elements or magnetic relays in the form of the nature, intensity, and succession of impulses controlling the servomechanics of the steering apparatus.

I draw my second example, for comparison, from the field of normal human motor co-ordination where all afferent organs function normally and the only unusual conditions are those of the motor problem. Fasten the handle end of a ski-stick in front of the buckle of a subject's belt. Attach a weight of 1–2 kg to the far end and on the right and left sides of the wheel attach a length of rubber tubing long enough to allow the ends to be held in the subject's left and right hands. Instruct the subject, turning the stick point

forwards, to stand before a vertical board on which a large circle, square or other simple figure has been drawn, and to try, manipulating the ski-stick only by pulling on the rubber tubing, to follow the contours of the figure with the point of the ski-stick. The stick here represents one segment of an extremity with two degrees of freedom; the tubing is analogous to two antagonistic muscles introducing a further two degrees of freedom into the system. This experiment (which is very useful for demonstrations in an auditorium) makes clear to all who attempt it just how difficult and complicated it is to control systems which require the co-ordination of four degrees of freedom, even when under the control of a human being in possession of his full complement of receptors, but without motor practice with this task, who has been dealing with his bone-muscle motor apparatus from the first weeks of his life.

The definition of co-ordination which I have given in previous accounts still appears to me to be comprehensive and accurate: *The co-ordination of a movement is the process of mastering redundant degrees of freedom of the moving organ, in other words its conversion to a controllable system.* More briefly, co-ordination is the *organization of the control* of the motor apparatus. In the basic definition I have deliberately not discussed the reinforcement, inhibition, etc., of the redundant degrees of freedom, but their mastery. This is because (as extensive work on children, sportsmen, and also hemiparetic subjects and amputees [9, 14, 21, 65] has shown) fixation eliminating the redundant degrees of freedom mentioned above is employed only as the most primitive and inconvenient method, and then only at the beginning of the mastery of the motor skill, being later displaced by more flexible, expedient and economic methods of overcoming this redundancy through the *organization* of the process as a whole. The importance of the role played by the organization of the control of interactions, even in the simple case of the control of only two degrees of freedom, is already apparent from our first example of the automatic control of a car along a road. It follows, from the definition above, that co-ordination cannot be regarded as some sort of independent activity—as a particular act directed at the external world. It is better to regard it as a means of ensuring responsiveness and flexibility of execution in the motor system; it may be regarded as a type of *motor servomechanism*.

In studies on the structure of movements I have thoroughly considered the reasons which emphasize the biodynamic necessity for the organization of the mechanisms of motor co-ordination on the ring principle. I have also described some aspects, revealed by observation, of those physiological processes of interaction in control which effect the co-ordinational guidance of a movement through the mediation of sensory syntheses of various levels of structural complexity. We saw how important, among the unpredictable and almost independent forces which must be perceived and overcome, is the part played by *reactive forces* which occur together with external forces, which are inevitably produced in movements of the multi-linked kinematic chains of the motor organs, and which are complicated in exponential progression by each additional link in a series of joints and by each new degree of freedom of movement. We shall not discuss this purely biodynamic side of the problem any further at this point (see Chapter III).

We now turn to a question which has been left obscure in the studies above but which has become increasingly pressing in the context of contemporary developments in physiological thought. If motor co-ordination is a system of mechanisms ensuring the *control* of the motor apparatus and permitting its rich and complex flexibility to be utilized to the full, what can we say at the present time about the means and mechanisms of this *control* of motor acts? How may the regularities we now observe in this control be employed in the interests of applied cybernetics, and which aspects or properties of these regularities can be isolated as most specific to the nervous systems of the higher animals and of man, so that we may more precisely illuminate the gap which still qualitatively divides (and clearly will divide for some time to come) such processes as may be attained by automata from those which are realized in the motor acts of the life processes of highly developed organisms?

We must first briefly deal with some problems of terminology and attempt to systematize the principal types of self-regulating systems which are known at the present time (from here on we shall for brevity indicate this term by its first letters S.S.) and list the problems and topics in which we are interested.

All systems which are self-regulating for any given parameter, constant or variable, must incorporate the following elements as minimum requirements:

(1) *effector* (motor) activity, which is to be regulated along the given parameter;

(2) *a control element*, which conveys to the system in one way or another the *required value* of the parameter which is to be regulated;

(3) *a receptor* which perceives the *factual* course of the *value* of the parameter and signals it by some means to

(4) *a comparator device*, which perceives the discrepancy between the *factual* and *required* values with its magnitude and sign;

(5) *an apparatus* which encodes the data provided by the comparator device into correctional impulses which are transmitted by feedback linkages to

(6) *a regulator* which controls the function of the *effector* along the given parameter.

In this way the entire system displays a closed circle of interaction, the general scheme of which is given in Fig. 31. Between the elements which have been enumerated there are frequently included auxiliary devices of secondary importance such as amplifiers, relays, servomotors, etc.

The short terms used by German authors for values of the parameter to be regulated are very convenient and we also find it expedient to use them. The *required value* will in future be designated as Sw (from the German *Sollwert*), the *factual value* as Iw *(Istwert)*; the *discrepancy* between these which is perceived by element 4, or more exactly the excess or difference of Iw over Sw ($Iw - Sw$), will be designated by the symbol Δw.

As an example given by Wiener [77] from an idea by his partner Rosenblueth the co-ordinational control of the act of seizing a visible object from a table top may be regarded as a constant process of estimation of the rate of diminution of that section of the path over which the hand must still travel to meet the object under consideration. We have every justification to designate the position of the object as Sw, the current position of the hand as Iw and the regularly diminishing distance between them as the variable $\Delta w(Iw - Sw)$. I must explain that both in the explanation above and henceforward, I shall regard the co-ordinational process in terms of *micro-intervals* of its track and of time, basing this treatment on data which have been accumulated over years of work by my colleagues and myself. For this reason I shall regard in this

respect the *continuous planned path or process of movement of an organ* as the variable Sw and the factual variable coordinates of the latter as Iw. In the present context Δw will be the threshold values of deviations which are more or less accurately corrected
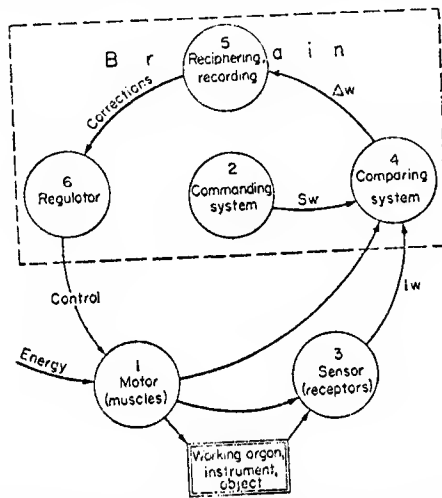

FIG. 31. The simplest possible block diagram of an apparatus for the control of movements.

during the course of the movement, as an example of which we may take the deviations of lines drawn by hand with a pencil or the point of a planimeter from a ruled line which a subject is set to follow. Consequently, in our sense Δw is not a systematically diminishing macro-distance, but oscillates in value, increasing and diminishing with the attainment of small values of variable sign and direction.

The central command post of the entire S.S. ring system is naturally its control element 2. Depending on the character of the Sw given by this element all conceivable types of S.S. may be divided into two large classes: S.S. with fixed constant values of Sw (so-called stabilizing systems) and S.S. with values of Sw which vary for one reason or other (tracking systems). The law of which the course of the change of the given Sw may be called the *program* of the functioning of the S.S. Changes between successive stages in the realization of a program may be stepwise or continuous,

and may, in various cases, be functions of time, of the path of action, of the working-point of the motor effector or of some intermediate resultant stage of operation, etc. In the most complex and flexible systems even the programs may be interchangeable.

Stabilizing systems are most primitive in their function and least interesting from our point of view although their analogues may be found in the operation of reflex-ring regulation among physiological systems. There are numerous examples of such systems in technology, beginning with Watt's centrifugal speed stabilizer for steam engines. A biological example is the pressure-receptor system of stabilization of arterial pressure which has been subjected to a thorough experimental examination from this point of view by Wagner [75]. The motor apparatus of the organism, in all its functions and in the very essentials of its biodynamics, is organized on the principle of an S.S. system of the tracking type with a continuous program of changes for successive regulations of Sw in each case.

All elements of the most simple scheme of circular control incorporated in our list and in our plan (see Fig. 31) must also necessarily occur in organic regulational systems in one form or another, most especially in systems of motor control. Our knowledge of these structural elements in the living motor apparatus is very uneven. We still know nothing whatever of the physiological properties, or even the neural substrates, of elements 5 and 6. The moving elements of 1, the motor effectors of our movements—the skeletal muscles—belong, on the other hand, to a category of objects which have been investigated by physiologists and biophysicists very thoroughly and in great detail. The operation of element 3 of the scheme—the receptor complex—has been thoroughly studied, but only from one point of view—as was shown in the first part of this report—and the aspect of its operation now under consideration still provides a great number of topics for investigation. I shall attempt to discuss here what can at present be said, both factually and hypothetically (with ordered degrees of probability), about the physiological structure of elements 2, 4 and 3 of the scheme for the control of motor acts; I shall also incidentally discuss as they arise problems which we have already encountered, though we are still very far from being able to solve them. It will be appropriate to begin this review with the "command point" of the scheme—with the control element 2.

Every intelligent purposeful movement is made as an answer to a

motor problem, and is determined—directly or indirectly—by the situation as a whole. Inasmuch as a motor act by the individual (an animal or human being) incorporates a solution to this problem, there is a basis of some program or other which will be realized by the control element. What is it that represents such a program of control for a movement, and by what is this program controlled in its turn?

In the monograph on the structure of movements [23] I discussed in detail *how* sensory corrections arise and *how* they affect the course of a movement. The topic raised here concerns a different problem which was almost ignored by the book referred to; *what* problem which was almost ignored by the book referred to; *what* *it is precisely* that is corrected, and *what* controls the process and the basis of such corrections.

Observation of the simplest movements, such as those in the category of isolated movements (drawing straight lines through the air, indicating a point, etc.), may give the impression that the guiding principle underlying the program of changes in Sw, by means of which corrections to the movements are realized, is the geometrical form of such movements: the observation of linearity if it is necessary to describe a straight line, the observation of direction when indicating a particular point, etc. In coming to this conclusion, however, we fall into the error of mistaking the particular for the general. In the forms of movement described above it is indeed true that correction is effected by means of a geometrical image, but only because this is precisely the point of the problem. In the second of the examples which we have given (i.e. that of pointing), the geometrical guiding element of the movement has shrunk to a single point in the visual field. It is quite sufficient to be acquainted with cyclogrametric records of the movements of pointing with a finger at an object, carried out with optimal skill and accuracy, to become convinced that N successive gestures by the same subject are made through N non-coincident trajectories which only gather, as at a focus, in the vicinity of the same required point which is being indicated.* This means that the geometrical principle of correction is restricted, as far as possible, to the determination of the minimum extent of a movement which is absolutely necessary, and gives way in the remaining parts of the movement to some other guiding principles. The reliability and speed of their courses and their faultless coincidence on the target provides evidence that such principles are

* Cf., also, Fig. 21.

certainly incorporated in each micro-element of the gesture of pointing. (Compare this movement with one of a patient with ataxia!)

The error of mistaking the particular for the general becomes obvious as soon as we turn from movements which are geometrical in respect to their goal to motor acts of another type. If we consider relatively simple specialized motor acts which are repeated many times and so become, as the term is, automatized, we may be sure that the attainment of their motor goal (locomotion in sport, industrial processes, etc.) is adequately achieved much earlier than the automatization of the movement and its stabilization to a significant degree of geometrical consistency. In many cases the goal of the movement is attained at the very first attempt. It follows that the kinematic motor composition of an act is by no means a universal invariant which guarantees the success of the action to be fulfilled. If we turn from the simplest and most repetitive actions to more complex purposeful movements, which are frequently multiphasic and conditioned by the need to overcome variable external conditions and resistances, such broad variations in the motor composition of movements become a universal rule.

If the program of a motor act is discussed, as a whole, in macroscopic terms we cannot discover any other determining factor than the image or representation of the result of the action (final or intermediate) in terms of which this action is directed and which leads towards the comprehension of the corresponding motor problem. In particular, how and by what physiological means the image of the envisaged or required effect of the movement may function as a guiding principle of the motor structure of an act, and as a program for the direction of the effector element, is a problem to which there are as yet no signs of any concrete or determinate answers. Whatever forms of the motor activity of higher organisms we consider, from elementary movements to multiphasic industrial processes, writing, articulation, etc., analysis suggests no other guiding constant than the form and sense of the motor problem and the dominance of the required result of its solution, which determine, from step to step, now the fixation and now the reconstruction of the course of the program as well as the realization of the sensory correction.

The fact that I have referred, as the characteristic guiding principle of the motor act, to the understanding or the representation of the result of an action (which is a topic for psychological investigation),

and that I have emphasized that we do not yet understand the physiological mechanisms at its basis, does not mean that we can never understand the essentials of these mechanisms, or that we must not give them our attention. We are already in a position to consider the undivided psychophysiological unity of the processes of the planning and co-ordination of movements, and to apply a determinate terminology to the psychological aspects of the necessary control factor, while as physiologists—lagging behind psychology in the forefront of the study of movements (as we said above)—we are unable to analyse the physiological aspects to these processes. However, *ignoramus* does not signify *ignorabimus;* and the very title of the present chapter emphasizes that its purposes were rather to raise and formulate unsolved subsidiary questions than to answer those already propounded.

In Chapter 8 of the book referred to in ref. 23 there was a thorough discussion of how, and under the operation of what causes, the motor structure of movements which are repeatedly carried out may be formed and stabilized during the development of so-called motor habits through practice. As a brief extract we may here emphasize that even in the case of such uniformly repetitive acts the variability in the motor picture and in the range of initial conditions may at first be very great, and a more or less fixed program develops depending on the extent to which a motion is practised, and by no means at the first attempt. The process of practice towards the achievement of new motor habits essentially consists in the gradual success of a search for optimal motor solutions to the appropriate problems. Because of this, practice, when properly understood, does not consist in repeating the *means of solution* of a motor problem time after time, but in the *process of solving* this problem again and again by techniques which we changed and perfected from repetition to repetition. It is already apparent here that, in many cases, "practice is a particular type of repetition without repetition" and that motor training, if this position is ignored, is merely mechanical repetition by rote, a method which has been discredited in pedagogy for some time.*

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* In exercises in sports and gymnastics, the motor structure (referred to as style) is incorporated as an integral part in the meaningful aspect of the given problem. For this reason it is one of the primary objects of the trainer to achieve as determinate a formulation and as rapid a stabilization of the motor structure as is possible for his pupil, but this does not in any way contradict the position maintained above as to the correct definition of practice.

It is possible to be a little more concrete in one's statements in regard to the *microstructure* of the control of continuously flowing motor processes. In whatever form the general guiding directives of the anticipated solution are decoded into the concrete, detailed Sw elements of direction, forces, velocities, etc., of each limitingly small (more exactly, threshold value) section of the movement, it is beyond dispute that in the subordinate sections of the effector complex there exists a corresponding version of Sw broken up into details in this way. It must be observed that the impingement of each current proprioception (in the broad or in the functional sense of the expression) upon successive momentary directing values of Sw provides at least three different types of information, all equally important for control. Firstly, one or another degree of discrepancy between Iw and Sw (Δw) determines, on passage through the ring system, the necessary correctional impulses; this part of the process will be more thoroughly studied in discussions of the "comparator element" (No. 4 in our list). Secondly, the information which is provided by the receptors as to the particular point of succession attained by the realization of the motor act incorporates the excitatory impulse for the transfer or switching of Sw to the next micro-element of the program in the train; this aspect of function is mainly reminiscent of what Anokhin [4, 5] has termed sanctional afferentation. There is, finally, a third side to the process of reception—apparently one of those phenomena which may be adapted to perceptual models only with extreme difficulty. In every act of movement related to the overcoming of independent and variable external forces the organism continually encounters complications which are irregular, and in most cases unpredictable, which disrupt the course of the movement from paths which are set up in advance by programs. It is impossible, or at least extremely difficult, to master these by means of correctional impulses integrated with the initial program of the movement, whatever this may be. In these cases the receptor information acts as the stimulus for the adaptive restructuring of the program itself "in progress". These may range from minor purely technical alterations in the trajectories of the movement to other adjacent paths, to qualitative reorganizations of programs which involve changes in the very nomenclature of successive elements and stages of the motor act, and eventually amount to the adoption of new strategies of solution. Such terminations and reconstructions of programs

as a result of receptor information occur much more often than one would expect, because they often involve only the lower levels of co-ordination and do not draw on the assistance of conscious attention (anyone who has walked, if only once in his life, on a surface that is not as level as a parquet floor will agree with this).

In the monograph on the structure of movements [23] it has been thoroughly demonstrated how numerous are the forms and ranges of correctional processes which, in the organization and mastery of a motor act, may be found to be distributed between interacting background levels of co-ordinational control. As was said in this book, what we describe as the *automatization* of a motor act is the constantly maintained transmission of numerous technical (background) corrections to the lower co-ordinational systems, the sensory syntheses of which are most adequately organized for corrections of the given type and quality. The general law, to which we know of practically no exception, that all component processes in control corrections disappear from the field of consciousness, besides being directly related to the guiding level connected to the very sense of the motor task, also provides us with evidence of the apportionment of correction in terms of levels which we call automatization. It is useful to emphasize at this point that in higher organisms (and in man in particular) there exists a rich and multisided sensorily equipped hierarchical system of co-ordinational levels involved in circular control both for the realization and for the momentary meaningful restructuring of various motor programs. This is clearly a consequence of the enormous number of degrees of freedom of the motor apparatus referred to earlier (which can only be controlled by a system as complex as we find here). This is also the underlying biological mechanism which permitted organisms having such a powerful central apparatus for motor control to develop their organs of movement during phylogenesis without being limited by the number of kinematic and dynamic degrees of freedom involved.

We must now turn to element 4 of the scheme given in Fig. 31. This element—the comparator device (as we have conditionally termed it)—is simultaneously a most interesting and puzzling physiological object, although the time is already quite ripe to begin its systematical investigation.

The ring principle of regulation is necessary in any mechanism which undertakes comparison of the current values of Iw and Sw, just as it is in all artificially constructed S.S. Some such system transmits an estimate of their mutual discrepancy (Aw) to subsequent stages of the regulating systems. This (Aw) is basic to the process of transmission of effector correctional impulses to the periphery. If there were no such functional system in the brain it would be impossible, acting on the basis of the Iw receptions alone, to provide for any sort of independently acting correction. Here we at once encounter a completely distinct process, by means of which we compare and perceive not differences between two simultaneous or successive receptions, (as, for example, in the case of measurements of the thresholds of differentiation for any given receptor), but between *current perceptions*, and the representation, in some form or other, of the *internally controlled element* in the nervous system (we do not yet precisely know whether this is a representation, an engram, etc.). The value of Aw is obtained as a result of this comparison. Because of this process we may discuss a separate threshold, the comparison threshold, as we may term it; in the most elementary cases this threshold is obvious, and easily accessible to measurement. So, for example, we have the threshold of the visual-vestibular correctional reaction at the beginning of the tilt of a bicycle from the vertical; the threshold which characterizes the beginning of the corrective movement of a pencil on a deviation from an imaginary straight line which has to be drawn between two points on a sheet of paper; the threshold for the control of the voice which may be obtained from the voice oscillograms of students learning to sing and attempting to hold the voice to a note of a determined frequency, etc. More interesting and typical features of the process under discussion will be given below.

One of the most important elements of control over the motor processes is the reception of currently occurring variations in Iw for *velocity*. The tachometry of artificial S.S. may be carried out on various principles which, however, always make use of some physical value directly measured by a particular apparatus, and directly related to velocity. (As an example we have the amount of friction on an armature of a spring controlled by the intensity of a magnetic field, etc.) It is essential for our purpose to recognize that receptors which are directly and immediately sensitive to changes in velocity do not exist in the organisms which we are considering. This prob-

lem, however, is solved in the central nervous system in some quite special manner, and clearly either by the same sort of comparator mechanism, or by an extremely close homolog to it, the reception of the momentary position of a moving organ being compared *with the trace* of the same reception of the momentary position at a preceding interval of time Δt. The value of Δt may be estimated (for the purposes of an orientational approach) as being of the order of 0·07–0·12 sec, as I shall try to demonstrate below.

If we consider the course of synthetic receptor processes of the most various types, then the phenomenon of *fresh traces* (as we have conditionally termed it), to which we have referred above, appears to be remarkably universal and of fundamental significance. In the visual perception of movements it would be impossible to perceive *not only the velocity but also the direction* of a given movement if the process of perception were not based on ceaseless *comparison* of current receptions with the fresh traces of immediately preceding ones. When we perceive a melody or a word aurally, we do not merely register the separate successive elements—the sounds—but also the time course of the melodic line, or the time picture of the phonemes together with their tempo. We can discriminate qualitatively between rising and falling sequences of tones, between the phoneme *Va* and the phoneme *Av*, etc. If I perceive, with my eyes closed, that a line is being traced with a pointer on my skin, I do not perceive merely the location, but also the *direction* of succession and the *velocity* of the movement of the pointer as two qualitatively distinct *properties*. These are perceived as being in some way primary. They appear to be primary or primitive to such an extent that they are in all respects qualitatively similar to raw sensations. These traces retain their active form only for a minute fraction of a second, so that fresh traces are sharply distinct from the usual phenomena of *memory*—which is the means of long term retention of centrally coded phenomena.

In a large number of cases the control of a movement requires the continuous perception not only of current *values* of this difference (Δw) but also of the *velocities* with which these differences increase or diminish. As Wagner [75] has correctly observed, often (for example in cases of small but rapidly increasing values of Iw), control is exercised precisely by means of perception of the velocity of change of Δw, because it is useful to react sensitively to the very beginning of the development of an adverse deviation even earlier

than the absolute threshold value of this deviation may be recognized and responded to. The indisputable fact that our sensory synthesis can also respond differentially to various rates of change of Δw is evidence that in the process of comparison under discussion the phenomenon of fresh traces must operate. The process of comparison is not, in this case, that of Iw and Sw, but of the fresh trace of their difference (Δw) occurring a fraction of a second earlier in time with a current value perceived at a given moment. In mathematical terms this is the process of the perception of the derivative $d(Iw)/dt$.

There is no doubt that the processes of perception of velocities and directions, the processes of comparison of Iw and Δw with their fresh traces for all dimensions of reception, etc., cannot in fact proceed *continuously*, but must rather do so in terms of differential intervals of time dt, there being some lower limit to the interval of time Δt which we may consequently regard as a threshold value. At the basis of these processes we find values of a particular type of thresholds, thresholds for *time*, which are clearly in very close physiological relationship both to the thresholds characterizing the speed of the psychomotor reaction and to physiological parameters such as lability, refractoriness, constants of adaptation, etc., which are clearly in need of immediate and intensive investigation. There is no doubt that psychologists specializing in the organs of sensation will already be in a position to criticize and to add material which is important to the argument in favour of the idea of fresh traces given above for the elucidation of the present problems.*

I should like to put forward the following notes towards a working hypothesis. In the thirties of the present century, M. N. Livanov had already found that the amplitudes of the peaks of the β waves on electroencephalograms vary considerably in magnitude from the peaks and troughs of the α waves, appearing, as it were, to be modulated by the latter. This fact may be taken as evidence of some sort of periodicity in the variations of excitability of the *cortical*

* In particular there arises the natural problem of the relationship which the mechanism of fresh traces bears to psychological mechanisms in the more general problems of engrammatization and of memory. Recent data suggest with ever increasing persuasiveness the paramount importance of the complex and many-sided nature of the biological processes organizing the reception and transmission of information. Further investigation shows how distinct are the phenomena of fresh traces from other earlier investigated forms of the function of retention of impressions, and of what the anatomic-physiological substrates of such impressions, etc., may be.

elements observed in the α *rhythm.* Grey-Walter [47] noted that the lower threshold limit for the fusion frequency for flashes, cinema pictures, etc., in the ocular apparatus closely coincides with the frequency of the α rhythm, and even varies in parallel to the latter in individuals. It also does not seem to be a coincidence that the lower limit of the fusion frequency for hearing at which the specific sensory properties of a *sound* can be discriminated lies at about the same range of frequencies. There are, moreover, some un-published orientational investigations by V. S. Gurfinkel on holding and movement in the unloaded hand (cf., also, [46]) and also a series of cyclogrametric observations by L. B. Chkhaidze on the rhythms of the acceleration impulses in the foot of a cyclist.* In both these cases the alternation of correctional impulses is in com-plete mutual synchrony, and falls within the limits of the same fre-quency band as the α rhythm, i.e. 8–14 c/s. Is there no reason to suppose that this frequency marks the appearance of rhythmic os-cillations in the excitability of all, or of the main elements of the reflex S.S. of our motor apparatus, in which a mutual synchroniza-tion through rhythm is doubtless necessary? We might also see in this light the ordering of the sensory and co-ordinational processes in terms of threshold values of the intervals of time Δt separating the moments of greatest refractoriness from the moments of maximal lability during which a momentary impression Iw is held in the form of a fresh trace until a subsequent rise of excitability. The distribution of the α rhythm over the entire surface of the cortex, its particular dominance in the receptor zones, and their synchronism with it over the whole of this range may also be taken as evidence in favour of this hypothesis. We may then describe the α rhythm as the pacemaker mechanism which gives to co-ordinational processes their determinate time parameter—their type of Sw of time, and intervals of Δt—as a regulating internal physiological pendulum appearing in these processes, such as that which British physiologists describe as a pacemaker. It must naturally be em-phasized that whether this pacemaker is related to the α rhythm or not it has great physiological importance. There is an urgent need for quantitative investigation and for the determination of its relationships with such psychophysiological indicators as simple reaction time, the personal equation, etc.

* I must express my debt to V. S. Gurfinkel and L. V. Chkhaidze for these personal communications.

It remains for me briefly to describe one more characteristic of the co-ordinational process which is closely related to the pheno-menon of fresh traces and to the parameter It.

Situations are encountered in the processes of motor control in which great, sometimes decisive, importance attaches to cor-rection of an advance or anticipatory character. This is particularly the case where, during the course of any given segment of a move-ment, retrospective control becomes practically impossible. There is a whole class of such motor acts (so-called ballistic movements) whose existence is only made possible by means of this type of antici-pation: throwing at a target (throwing stones, spears, all possible ball games, etc.), jumping across a ditch or a high obstacle, a sweeping blow with a heavy hammer, etc. We must also note the existence of analogous anticipation in a number of similar motor acts, where it necessarily co-exists with corrections of a usual type; these are *movements which forestall others,* similar to those made by hounds following a wild animal and making rushes which are di-rected, not towards the momentarily visible position of the quarry, but across, towards an anticipated or extrapolated point of inter-section with its trajectory. There are many examples of this sort of thing—catching a moving object with one's hand, pas-sing a ball to a running team-mate, interposing a racket across the path of a moving ball or spheroid as in the game of table-tennis, and many others. Mittelstaedt [58] proposes that these two types of correction be distinguished from each other, and that they should be regarded as two equally important classes which he terms *Regelung* and *Steuerung.* Another category is more important in the present context.

The existence of correction of the anticipatory type, and the fact that we encounter it much more frequently than appears at first sight, directs our attention to the importance of anticipation in realizing any type of goal-directed motor act. Programming, as has been demonstrated above, is determined by the apprehension of motor problems as they arise, and represents an anticipation both of the result which is determined by its solution, and of such motor techniques as are necessary for its attainment (the latter if only in the most general terms). Many psychophysiological processes are entirely based on a similar "sight into the future". These have been termed "sets" and only in recent years has the term come to attain its full significance. Just as an analysis of the operation of the "setting or

commanding complex" 3 reveals an hierarchical range (of levels of operation) beginning with the organization of the program of the motor act as a whole, and extending down to the level of the most detailed "micro-*Sw*" from moment to moment, or from Δt to Δt, we cannot now avoid the conclusion that in order to guarantee the completion of the micro-elements of the program and to undertake the direction of the motor process the successively emitted *Sw* must always *precede the actual movements*, preceding them if only by the threshold interval of time Δt. This is, however, enough to ensure that the equilibrium destroyed in this way (between the attained *Iw* and the future intended *Sw*) guarantees the dynamics of striving towards the end result. So, speaking semi-figuratively, the current micro-regulation of movements shuttles constantly between the present moment t and the limits of the interval from $t - \Delta t$ ("fresh traces") to $t + \Delta t$ (the anticipatory *Sw*).

I have brought together in these pages a number of problems related to the regulation of the life activity of the higher organisms, prompted by the analysis of motor acts. In the following chapter, I shall consider critically such current or imminent problems as the function of the coding organs, the interdependence between discrete and wave-like processes in the central nervous system, and, finally, some new prospects in the direction of the application of mathematics to the physiology of the activity of the nervous system.

CHAPTER V

TRENDS AND PROBLEMS IN THE STUDY OF INVESTIGATION OF PHYSIOLOGY OF ACTIVITY

NEW concepts and problems which have arisen out of the development of cybernetics have powerfully seized the attention of physiologists. The overwhelming majority of these problems appearing in our physiological journals indicate a desire to establish a *rapprochement* between the current state of cybernetic theory and the attitudes and achievements of classical Russian physiology. This forces us to consider the history of the subject intently and thoughtfully. It seems, however, that the uninterrupted development of strictly materialistic concepts and points of view which are our heritage from native physiologists of the schools of Sechenov, Pavlov, Vvedenskii, Ukhtomskii and others depends on their further integration into the contemporary body of biological science. It is now more important to look ahead, and to attempt to discern, though perhaps only in the most general terms, *problems* (though still remote from a solution) deriving from the new facts and concepts, and some new *directions* which still need to be carefully considered, but which, it seems, may allow us to attain the discovery of new and wide horizons. We may justifiably relate the study of the *physiology of activity* to these new directions of investigation.

I

The classical physiology of the last hundred years is characterized by two sharply defined features. The first of these is the study of the operation of the organism under quiescent inactive conditions. Such conditions were artificially secured wherever possible by decortication, by anaesthetization of the animal, or by fixing it in a stand under conditions of maximal isolation from the external

world. This analytical approach to the study of quiescent conditions derived from the attempt to study every organ and every elementary process in isolation, attempting to exclude side effects or mutual interactions. In general terms this approach corresponded to the predominance of mechanistic atomism in the natural science of that era. The absolutism of that point of view led to the conviction that the whole is always the sum of its parts and no more than this, that the organism is a collection of cells, that all behaviour is a chain of reflexes, and that a sufficient acquaintance with the individual bricks would be enough for the comprehension of the edifice constructed from them.

The second characteristic feature consisted of the concept that the organism exists in a state of continuous equilibrium with the universe surrounding it, and that this rigid equilibrium is maintained by means of appropriate reactions, unrelated to each other, and made to each successive stimulus impinging on the organism from the surrounding environment. The whole existence and behaviour of the organism was visualized as a continuous chain of reactions on the stimulus–response model (nowadays we would talk of input and output). The standard of the classical materialistic physiologists was the *reflex arc*, and their central aim was the analysis of regularities in *reactions* considered as rigidly determined input–output relationships.

The general technico-economical conditions maintaining after the First World War sharpened interest in the *working* condition of the organism. New branches of applied physiology arose—the physiology of work and physical exercise, psychotechnics and biomechanics. Naturally interest began to be directed towards the physiology of movements (here, and from this point on, we shall use this term to indicate goal-directed motor acts, and not insignificant fragments of movements such as the withdrawal of a paw because of pain, or the knee-jerk reflex). If this department of physiology has not been given sufficient weight and attention in the pages of the older physiology of rest and equilibrium, its preeminent importance now began to be apparent. In fact movements are almost the only expressions of the life activity of the organism. Movements are the means by which it does not simply passively interact with the environment, but actively *acts upon it* in whatever way is necessary. Sechenov had already indicated the general significance of movements in his remarkable book *Cerebral Reflexes* one hundred years ago. If we add that time has since revealed the

integral nature of the participation of movements in all acts of sensory perception, in the education of the sense organs during early childhood, in the active development of an objectively consistent *world image* in the brain by means of the regulation of perceptual *synthesis* through practice, it is easy to understand the displacement of the centre of gravity of interest which is becoming increasingly felt in contemporary physiology.

The progressive growth in the complexity and power of technical devices has demonstrated very clearly that problems of control and regulation form an independent area of study—a study which is in no way less complex, important or comprehensive than that of the energies which are subordinated to these controls. The problem of the rider has begun to overshadow the problem of the horse.

Analogously in physiology, beginning with a study of the energetics of the operating (working) condition of the organism (gas exchange, the control of secondary systems which do not directly participate in external work—breathing, circulation, sweating, etc.) interest has gradually begun to centre on the more comprehensive problems of the regulation and central control of the activity of living organisms.

II

For further discussion it is necessary to pause briefly on one particularly important feature of the control of motor acts which has been established with complete objective reliability for both animals and men.* This is the fact that the relationship between the *result*—for example, the movement of a limb or of one of its joints—and such commands as are delivered to the musculature from the brain through the *effector nerves* is very complex and nonunivocal.† This absence of univocality is a result of the fact that

* For a bibliography enabling the reader to become better acquainted with experimental and clinical data see the author's paper on "Immanent problems in the theoretical physiology of activity" in the textbook *Problems of Cybernetics*, publ. 1961, and the journal *Voprosi Psikologii*, No. 6, p. 70, 1957.

† The indicated relationship between muscular excitation and the resulting movement is very different from the picture which was confidently described by physiologists of the last century (Bekhterev, Munk, etc.). It then seemed natural to treat the motor area of the cortex as a sort of keyboard on which somebody's hand, in sovereign control, described the program for a given motor stereotype. The pressing (excitation) of one of these cell buttons always brought about a given degree of flexion at a given joint, the pressing of a second brought about extension, etc.

muscles are elastic belts (imagine the connecting rod of a steam engine replaced by rubber, or by a spiral spring) and the effects of their action on the organ which is moved depends essentially on the position and the particular velocity of that organ at the beginning of the muscular activity. This absence of univocality is further explained by the fact that, as in any physical multijointed pendulum, involved and complex involuntary forces *(reactive forces)* arise in a moving limb. The lack of one-to-one correspondence between messages to the limbs and the actions produced at particular junctures is finally also due to the fact that any meaningful movements overcome external forces which are quite beyond the control of the participant (gravity, friction, the opposition of an adversary, etc.) and which cannot be predicted by him. It is clear that organisms, whose only channels of operation upon the surrounding world are commands given to their muscles, may achieve controlled movements serving a particular purpose only by means of continuous monitoring and control achieved by the participation of the sense organs. The physiology of the remarkable and varied signalling equipment with which the organism is equipped, located in the muscles themselves, in the joints, and in the observation post of the body—the head incorporating the distance receptors of vision, hearing and smell—is now well understood. This apparatus provides for perfectly accurate and continuous *circular control* (i.e. feedback control) and revision (i.e. correction) of movements, even of movements comprising such complicated multiple-jointed structures as our limbs, and effected by the non-rigid muscles which drive them.*

It is possible that these complex dynamic features of motor acts which have just been described are the reasons for yet another characteristic feature appearing most clearly in habitual movements; that is, the remarkable structurality and completeness of a motor act, which makes it impossible to treat it as an arbitrary collection of successive reflex elements (see Chapters II and III).

* Here we have a typical case of *control by means of negative feedback*, a device which is widely used in simple forms in modern technical devices. We may incidentally note that this principle of negative feedback control has been observed by physiologists in recent years to operate in the most various forms of control exerted by the organism—the pupilliary reflex, regulation of blood pressure, of the heart-beat, of chemical equilibrium, etc. It is now beyond any doubt that the most general and prevalent form of organization in live organisms is not the reflex *arc*, but the reflex *ring*.

We will not dwell on this feature at present. It is more important to turn to another set of characteristics of goal-directed movements which are still very far from clear, and which still require careful investigation. The analysis of the peculiarities of this group of properties allows us to find a bridge between the *physiology of reactions*, with which psychophysiologists have been exclusively concerned for some time, and *the physiology of activity*.

III

What is the standard invariable determinant of this involved structurality of motor acts which we have just discussed? We cannot suppose *effector commands* to be such a standard determinant. These commands are emitted into a system involving at least two types of independent forces (reactive and external forces), they act upon the organ through a non-rigid musculature, and they must also vary between very wide limits in order to accommodate to signals coming from the sense organs. These afferent (incoming) signals also cannot act as standard determinants, because signals giving the degree of match or mismatch between movement and effect can only be as variable as the cues which provide them, and, more importantly, the information which they contain is a description of "what is" and not of "what must be done". The brain mechanisms by which the signals giving the progress of a movement, are coded and deciphered, and the degree of mismatch between emitted commands and the operation of the required muscle at the required time, also cannot be considered for this role, because they are necessarily just as variable and non-standard as the codes which they transform.

All our long experience in the study of motor activity, of motor habits and of clinical disorganization has demonstrated with great clarity that the standard determinant both for the programming of motor activity and its effection and correction by feedback connections can only be the formation and representation of a *motor problem* by the brain in one way or another. The analysis of this concept, and of the wide circle of relationships and facts which it entails, will be the particular business to which the remainder of this chapter is devoted.

If we do not, for the present, avoid simple commonplace

terminology, then the sequence of the arousal and realization of any action of the class of so-called voluntary movements may be represented in the form of successive stages.

1. Perception, and the necessary evaluation of the *situation* and of its bearing on the individual caught up in it.

2. The individual determines in what way it is necessary to alter this situation; what, by means of his activity, the situation *must become* instead of *what it is*. The motor problem has already appeared at this stage. It is not difficult to guess that this motor problem must contain more information than is included in the bare perception of the situation, some of which is at least partially not present in the latter. Animals in a herd, or people in a crowd, may be confronted with the same situation, but the motor behaviour of each individual will be different. Examples of this may be readily found.

3. The individual must next determine *what* must be done and

4. *How* it must be done, and what are the available resources.

These two micro-stages already represent a program of the solution of the problem, and after these there follows the process of its actual solution in terms of motor activity. It is scarcely necessary to emphasize that the control and evaluation of successive moments of the actual activity, the variability of the situation itself, with the fact that it is, generally speaking, possible to program only rather roughly movements which have some duration in time, all explain the adaptational variability of programs and of acts, permitting changes ranging from small corrections to widespread alterations in strategy.

It would be false to suppose that the micro-stages in the transition from the situation to the act which have been described above are found only in highly organized nervous systems. The same stages must also necessarily be found in such primitive acts as, for example, the pursuit of live prey by predatory fish. In this case we also have a situation which is perceived in the necessary form and measure, and a motor problem with a program for its solution. The precise way in which either of these aspects of the process is coded in the nervous system of a predatory fish is quite unknown to us, but it is beyond doubt that neither consciousness nor a particularly high level of nervous organization is necessary for them to take place.

Concerning the topic of the higher information content of the problem in comparison with the actual perceived situation, we must add the following. From the point of view of the dependence of the actions of an organism on the stimuli which provoke them, or on the input in general, we may draw up an imaginary series in which we may rank all actions (confining ourselves here to the actions of human beings) according to their degree of dependence on such activating stimuli. At one end of the series we have movements which can be fully explained in terms of the stimuli which activate them. Among these we have all the so-called unconditioned or innate reflexes. We may also include all reflexes conditioned during life experience which are nevertheless dependent on the activating stimulus—reactions of the general class of *conditioned reflexes* found in humans and animals alike.

We may place next in our rank order, movements for which the stimulus or signal continues to play the role of an activator, but which have a meaningful content that is increasingly independent of the stimulus. For motor acts of this class the activating signal increasingly takes on the features of a trigger signal, analogous to the pressing of a button which sets in motion the whole complex process of firing a rocket, or to the interjections "hep" or "arch" after which follow sequences of activity which are very little related in significance to these interjections. Finally, at the other end of the series, we find acts for which the activating or triggering signal does not play a decisive role, and in which it may be entirely absent. These are actions for which the program, and also the initiative, are entirely determined within the individual, and which, with greater accuracy, may be described as the operations to which the term "voluntary movements" may properly be applied. It is not difficult to see that a progression along our scale coincides with the gradual shift from passive acts, to acts having an ever-increasing degree of active involvement.*

* Conditioned reflexes must be referred, not to the intermediate class, but to the first of the types described here, as in the case of established and differentiated conditioned reflexes a stimulus fulfils not only a *releaser* function, but also acts in an informational way, completely determining whether it will be followed by an appropriate act, by differential inhibition, or by an act of another type, etc.

IV

Now we shall see what can be said at present about the necessary concomitants of every act of translation of the perceived situation into a motor action—of the phenomenon which would be called "looking forward" in Chinese, and which in more scientific terms may be called *extrapolation to the future*. Indeed, planning a motor act (irrespective of the way in which it may be coded in the nervous system) necessarily involves the recognition in some form of the pattern of what must be, but is not yet, the case. In a similar way to that in which the brain forms an *image* of the real *external world*—an image of the factual situation at a given moment, and of situations which have been experienced in the *past* of which we have impressions in our memory—it must possess to some degree the capacity to form a representation of (or, what is the essence of the matter, to plan in advance) situations which are as yet unrealized, and which the biological requirements of the organism impel it to realize. Only such an explanatory image of the necessary future can serve as a basis for the formulation of problems and the programming of their solutions. It is certain that this image of the future is qualitatively very different from images of either past or present reality but, as the ensuing discussion will show, the possibility of its existence in some coded form in the brain (which need not in the least involve subjective consciousness), both in animals and in men, does not admit anything which is methodologically undesirable.

In a number of cases similar to the illustration provided and, it is possible, in experimental situations also, this "looking into the future" which we are discussing is accessible both to introspective observation and to chronometric measurement. We have, in the first place, cases where the program for meeting the motor problem is formulated as a physical code which is accessible to the sense organs. A musician playing by sight or any one of us reading a text aloud, advances his gaze some interval ahead of the notes or words sounded at any given moment. This is to say that both acoustic and psychomotor images of what is to be realized by motor means within a second, or fraction of a second, must be present in the brain all the while. It is possible, in this connection, to carry out an illustrative experiment on oneself. Try, without hurrying, to declaim to yourself (in the same way as reading to yourself silently)

any piece of poetry which you know well by heart. Mentally listening to yourself doing this, you will clearly perceive that two texts pass before the inner ear: one text in the tempo of the mental declamation, sometimes accompanied by lip movements which are often intense enough to be perceived, and a second which runs ahead, easily outstripping the first text, as if you are preceded, stanza by stanza, by some internal prompter. I have no doubt but that psychologists can suggest many more successful and fruitful types of demonstration for this phenomenon.

There is one very idiosyncratic group of phenomena, which have been observed on more than one occasion, indicating that the image of the future discussed here is not only limited to effects on the course of the programming of motor acts but may in certain cases possess a great physiological reality, as if this foreshadowing of the future already gave it an existence in the present. I have in mind sources of the *emotion of fear*, an experience which can be aroused solely on the basis of a clear image of the imminent future in the brain. In both ancient and contemporary scientific literature we encounter a whole series of descriptions of *death from fear*—so severe may be the autonomic-vegetative shock which is produced by this coded image. In literature we encounter examples of this in Gogol (*Vyi*) and Edgar Allen Poe (*The Fall of the House of Usher*).

In order to approach an experimental investigation of those principles by which the image of the future, in the widest sense of this term, may be coded in the brain—that is to say, the nervous processes serving as the basic guiding compass of the organism in all its behavioural manifestations—and its essential difference from the image of the present and immediate past, we must begin with a small theoretical discussion.

Let all elements of a given set E (of any number of dimensions) be related in terms of a determinate law to the elements of a second set J so that each element of the second set will be brought into correspondence with one or more elements of the first, and vice versa. We will refer to the set E in this case as the *primary image*, to the set J as its *reflection*, and to the principle or law of connection as the *law of reflection, or projection of E on J*. The elements of the primary set may (all or partly) be time functions. The elements of the set J would then be functions of time in the same way, and with them, the set J as a whole. Even the laws of reflection may be functions of time, and in this case the reflection J will be doubly

variable in time for both these reasons. As physical examples of systems of the type described we may take the optical image on the retina of a human being watching the movements in a street from a motor car. The continuously occurring changes in this image will be due both to the motions of the objects in the street, and to the changes in the law of optical projection on the retina of the eye because of the motion of the latter.

It is difficult for anyone who is not mathematically sophisticated to visualize the enormous number of possible laws of reflection amongst which we may search for the true law or laws of the formation of the image of the real external world in the brain. Meanwhile, repeated lack of information on theories, because of which the enormous number of such laws are naively reduced, has already frequently led both physiologists and clinicians to erroneous conceptions, sometimes to harmless errors, but often very far astray from a correct comprehension of the essence of the matter.

A characteristic example of such a discarded misunderstanding, is the problem of how we see objects in the external world the right way up in spite of the inversion of the visual field on the retina. This question attracted serious attention, and several hypotheses were put forward to describe a reinverting mechanism. The error in these explanations of the mechanism responsible for reinversion lay in the assumption of the separate existence of "percept" and "observer" in the brain. The former was in some way supposed to be reproduced element for element from the evidence available in the optical projection on the retina. The latter in some way perceived or saw this image, in a similar way to that of the subject seeing the external world. From this, it was a small step to postulate that this observer had his own visual area.

The error which has just been described has now already been exposed, and it has been mentioned only because it is instructive. Another important error is still alive and we must consider it.

V

The genesis of the concept of one-to-one correspondence between the cell network of the cerebral cortex and the elements of the perceptual fields of the organs of sensation—vision, hearing, touch,

muscle and joint receptors (proprioception)—is not difficult to determine. An enormous amount of material gathered from the experimental physiology and pathology of the brain from 1870 onwards (the date of the first discoveries in this area) indicated beyond doubt that not only was it the case that each type of sensation has its own corresponding separate *zone*, but that within these zones there was some sort of precise correspondence with the elements of the peripheral territory of a given sense organ. This correspondence was more or less highly differentiated depending on the particular zone involved. Among these projection areas of the cortex the most detailed appeared to be those subserving touch and proprioception, in which it was actually possible to trace a sort of cartographical projection (accurate, however, in very general features only) of the sensitive surface of the entire body.

The dynamic variability of the information from the sense organs, changing from moment to moment as it reached the primary projection areas of the cortex described above, forced investigators to postulate the existence of secondary zones alongside them which would subserve the functions of retention (memory) of sense impressions transmitted by the primary projection areas. It was assumed that these secondary zones had the same point-to-point projection characteristics as the former.

In order to turn now to the analysis of the error of atomism which is inherent in these postulates, which clearly was in great part a result of inadequate information in the field of projection theory, and which was discussed above, we must again make a small digression.

It is not difficult to demonstrate by means of two or three extremely simple visual examples that there may indeed exist pairs of sets such as project fully upon each other, but that while each of them is easily and completely divisible into its component elements, a relationship in terms of projecting elements, such as described above for the projection of the type E on J, leads to an obvious absurdity.

A blueprint for a machine is made up of a thousand lines. In order to make this machine the craftsmen must carry out a thousand operations. Does this mean that the matching of every line demands a separate operation?

I make a statement containing 1000 words. My opponent entirely refutes my case, also in 1000 words. Does it follow from this

that each of the words which he uses refutes one of the words in my statement?

Or finally, 1000 people read a book of 1000 pages. May we understand from this that the first reader reads page 1, the second page 2, and the hundredth page 100?

The technique of *reductio ad absurdum* is often a very useful device for the detection of an erroneous line of thinking.

Armed with the preceding examples let us turn again to the discussion of the basic position of the theory of the secondary fields, after which we may attempt an approach to a theoretical generalization of what has been said above.

What do we feel, touch or perceive with each of our organs of sensation? Things, objects. What are the elements of the multitude of environments which we encounter? Objects. What must be the elements for a cerebral projection of the type E on J in the corresponding cortical systems and in their cells? It is clear that it must be objects which figure here, both as separate reflections by the brain of the elements of the external world and as the stimulus signals for reactions to it.

If the erroneous nature of discussions of the brain image in these terms is not already clear enough from what has been said, we may proceed further along these lines.

A type of brain function which is the monopoly of man alone is articulate *speech*. We already have a collection of representations of the external world in the form of the first signal system. But words are the names of objects, so that it is necessary to add yet another projection in terms of elements arising out of this signal system, and we will obtain a second signal system, so to say, a projection of a projection, in which every object signal, image element of the first system will have its corresponding name in the second. Clearly, atomism has a very powerful hold upon the imagination if there still exists such an interpretation of the second signal system as reduces speech, the inexhaustibly powerful tool of thought, which no less than the hand makes a man a man, to the level of a dictionary of terms for concrete objects in the nominative case singular. Neither space, nor the aims of this statement, allow us to develop the theme we have touched upon. We shall accordingly limit ourselves to two or three questions. (1) In the second signal system what exactly are the signals for which such elements as "again", "twice", "γ function", "without", "indeed" and "or"

stand? (2) How and where in the atomistic second signal projection system are such signal words as "you think, he does not think, we will think, you would think, they will not think" incorporated into its structure? (3) Is it perhaps better not to discuss at all such verbal signals as "wave function", "quaternion", "antinomy", "transfinite"?*

An example of the same category of erroneous connections between two sets which are indisputably divisible in their elements, and also indisputably related to each other, is found at the boundary between psychiatry and neurosurgery. That is, the theory of psychomorphologism (now exposed as an error, and discarded) which classified and subdivided elementary psychic functions and the symptoms of their deterioration in relation to their connection with determinate locations in the brain. In this case also we can trace the confusion to the same error, which, in reference to the first of the examples of absurdities which we provided, we may term the error of the "blue print and the machine".

VI

Now, to turn from illustration to generalization: let us suppose that there are connections between the elements of the set E, which in one way or another join these elements into subsets by determinate laws, or even that we ourselves impose such ordering laws on the set as divide it up into families or subsystems of elements. The simplest example of an operation of this sort is the relation of a system of coordinates to a plane or a spherical surface. It is possible to give many examples of such sets in which an ordering of this type is not imposed from without, but exists within the set itself, and it is only necessary that the system should be observable and describable.

* The most convincing example of the inconsistency of the second signal system theory arises out of a practical problem. It must be pointed out that it has been quite impossible so far to use the results of many years' attempts to delineate the second signal system as algorithms for machine translation, whereas a true physiological theory of speech and language ought to play a leading role. A comprehensive analysis of the essence of this argument and the reasons for it are given in L. Uspenskii's *Word about words*, Ch. 6, p. 283, Molodaya Gvardia, 1960. Also in O. Kulagin's paper "On the operators describing the algorithm of translation" in the textbook *Problems of Cybernetics*, 2nd edn., p. 289, 1959.

Let us now suppose that the elements of a given set M are related, not to separate elements of E (as was the case in the projection of E on J in terms of sub-elements), but to whole subsystems of its elements—representing their systematic ordering. In cases of this type we will describe the set M as *a model* of the set E, and the principle of the given ordering and relationships as *the operator of modelling*.

It is not necessary to emphasize how varied the forms and principles of modelling may be. In some cases, to every function of the families making up the set of the first order E there corresponds a determinate in M (termed the functional). In other cases the operator of modelling determines an ordering or a grouping of functions of the primary set, in series, either continuous or discrete, so that such a series answers in M a certain type of a "function of functions". The very forms of selection of representative functions from the first set may be qualitatively very different from each other. The representations in the model may include exhaustively all the endless multiplicity of systemal functions which cover the first representation, or they may select discretely among them (for example, selecting only integer numbers as values for their parameters, etc.). This may also relate to each element or any constellation of elements in the model—discrete function axes of the first representation E—incorporating probability determinations of the strips of territory along them, etc. It is now necessary for us to formulate some basic points emerging from all that has been said so far, and which directly bear on our theme.

In the first place, describing this widening of the limits of the principle of representation, we may affirm with confidence that in the brain a *representation* (or representations) of the world is *constructed along the principles of a model*. The brain does not receive an impression of the external world in the form of a passive inventory of elements, and does not employ such primitive means of subdividing the world into elements as first come to mind (phrases for words, and plans for drawings), but applies to them such operators as most accurately model the world, casting the models in the most consistent, exact and comprehensive forms. This process, or act, of mentally modelling the world is, under all circumstances, undertaken *actively*. In reality if the principles of analysis, systematization and reflection of the set by the system are applied to the primary image by the brain itself, this process of the formation and

use of operators is active by its very nature. And if the regularities in the internal ordering of the set E are inherent, then it is only possible to note them, recognize their significance, and employ them in the capacity of operator principles by means of active observation and investigation.

Something more may be said about the general characteristics and properties of active operational modelling of the external world.

Imposing on the first representation E one or other systematic regularity, or formulating a regularity which is already observed in the first representation, the brain brings some degree of additional information to the task, and by this means the information we obtain from the first representation is quantitatively extremely economized, but enriched in its meaningful content. It is possible to compare this additional information introduced from within to an enzyme, a small quantity of which, secreted by the organism, produces the optimal conditions for the digestion of a large quantity of a food.

It becomes clear in passing that the arguments hypothesizing an internal isomorphic representation of the sensory periphery (the retinae, skin, etc.) are false in principle, and cannot be accepted as circumstantial evidence for the existence of the observer in the brain whom we described above. The consequent duality of the observer and the percept, which alone of all schemes requires this detailed isomorphism, becomes superfluous and unnecessary from the point of view of active operational modelling. A model does not contemplate anything which confronts it from without, but is a coalescent indivisible unity of processes and mechanisms transcoalescent indivisible unity of processes and mechanisms transforming received information, which constantly changes without losing its continuity, or unity, and directs the course of the active behaviour of the organism.

The phenomenon of looking into the future which has already been mentioned as the basis for every motor problem (or, as we may now say, for every *model of the future*) forces us to recognize that in the brain there exist two unitary opposed categories or forms of modelling the perceptual world: the model of the past–present, or what has happened and is happening, and the model of the future. The latter proceeds directly from the former, and is organized in it. These are necessarily distinct from each other, chiefly because the first type of model is single-valued and categor-

ical, while the latter can only operate by means of extrapolation to some or other *degree of confidence* or probability.*

Problems related to the model of the present lie beyond the scope of this paper. Many psychological investigations have already been undertaken along these lines. We shall limit ourselves to a single example which may incidentally indicate the great practical importance of explanations of the nature of operators and operational models of the objects of the perceptual world. This example concerns the processes underlying the perception of *configurations*.

The visual image of a circle has five degrees of freedom (or represents a five-dimensional continuum) in terms of the multiplicity of its optical projections on the retinae. A triangle has six degrees of freedom, while the projection of the letter *H* has twelve, and the projections of some of the other letters of the alphabet have even more. This does not, however, prevent the operator processes in the brain (although their structure is quite unknown to us) from correlating the enormous variety of such optical projections and (we may suppose) of cortical projections, with a single meaningful code of symbols. There can be no doubt that when it is possible in the future to build a machine modelling this process which will recognize *letters* irrespective of their sizes or type faces, it will surely operate not by means of passive *scanning* (as do present experimental examples), but solely in terms of the cerebral principles of operator modelling, when these are understood.

* It is interesting to note that the two aspects of models of the surrounding world co-existing in the central nervous system are very clearly connected localizationally to different parts of the hemispheres. The neurosurgical clinic brings evidence of the contrasting forms of disturbances resulting from the lesions in the posterior and the anterior parts of the cerebral cortex. Lesions of the lower parietal fields, surrounded with the primary and the secondary zones of principal categories of reception (vision, hearing, touch), bring with them all sorts of disturbance in the simultaneous perception, in the ordering of objects and movements *in space*, briefly, in the structural synthesis of sensory information which are all the essential features of a model of factual'y existing reality. On the other hand, in the clinics it is demonstrated that with prefrontal and frontal lesions there are various types of loss in the planning and programming of active behaviour, in ordering the links of the chain of a motor act *in time*, in the chief premise of every form of activity, the so-called orientation reaction—that is to say the orientational prognosis of surrounding events and changes. All these forms of nervous activity indisputably belong to the domain of modelling of the future in the sense discussed above.

VII

That important form of cerebral modelling which was only recognized by investigators after the arousal of interest in the physiology of activity—that is, *the modelling of the future* to which we now turn—is logically possible only by means of *extrapolation* from whatever the brain is able to select from the current situation, from the fresh traces (see Chapter IV) of immediately preceding perceptions, from the entire previous experience of the individual, and finally from those active trials and assays belonging to the class of actions which have so far been summarized briefly as orientational reactions and whose fundamental significance has certainly been underestimated.

The complex of nervous processes which makes up a model of the future is so unclear and enigmatic that very little can be said about it. Apart from the indisputable statement that such a complex exists, and plays a most important directional role in the active perception of the surrounding world, as has been described above, we may make the following observations.

In sharp distinction to the model of the present the model of the future has a *probabilistic* character. The anticipation or expectancy of the possible outcome towards which the current situation is moving is only possible by means of extrapolation and never, generally speaking, can be brought to a categorical result. At any phase of this process the brain is only in a position to survey a sort of table of probabilities for possible outcomes.

Outcomes	A	B	$C\cdots$	$M\cdots$	X	Y
Probabilities Motor problem	P_A 0	P_B 0	$P_C\cdots$ 0$\cdots$	$P_M\cdots$ 1$\cdots$	P_X 0	P_y 0 $\Big\} \Sigma_\varphi = 1$

It is hardly necessary to make the point that, in the interests of analysis, we have restricted ourselves to a very simplified schematization.

Meanwhile, the motor problem which the individual determined for himself is formulated as a categorically unique outcome of the current situation, whatever its *a priori* probability may or may not be in the table (even if it is equal to zero). In this way the organism's activity is directed against the probabilistic model of the future, and

the determination of problems that arise is the dynamic struggle of the individual to raise the probability P_M of the desired outcome until it reaches unity, or becomes an accomplished fact. This struggle implies the reduction of the probabilities of all other outcomes to zero. It is clear that this struggle must result in the lowering of the entropy of the system involving the individual and his immediate environment, that is to say, this must always be a process endowed with *negative entropy*.

The struggle described above takes place in a complex field of conditions with a multiplicity of variables. In the first place, the extent to which the brain is able to make successful extrapolations, and its estimation of perspective and of possible outcomes must necessarily be very approximate. (It is, however, probably no more approximate in relation to the requirements of a given living creature, in the case of extremely elementary organisms, than in the case of creatures with very highly developed brains.) The coarseness of the possible extrapolation must necessarily increase with the interval of time, Δt, over which the organism attempts to exercise foresight. In the second place, the success of the extrapolation also depends on the term which the subject sets for its completion. If conditions are rapidly changing, and the organism is involved in time trouble, it may be obliged to limit itself to primary, coarsely exploratory techniques and responses, since it does not have sufficient time for more accurate ones. However, even when caught up in the toils of a threatening situation, where time is important, the selection of strategies of behaviour always involves a choice between responses which may be rapidly effected, though these may also be less accurate, and slower responses which have been more reliably evaluated. Thirdly, and finally, the field of conditions encountered by the organism is itself variable in time, and is both dependent on, and independent of, the activity of the individual, so that the organism is, in fact, constantly involved in a sort of conflict situation with the environment. It is already apparent from the foregoing that the evolution of Theory of Games is of great importance to the physiology of activity.

Among the related questions which require the combined attention of physiologists and mathematicians is the problem of the forms of extrapolation which are employed by the nervous systems of organisms of high and low development, and the particular mechanisms which they employ to achieve this guidance. Considering the

lower, purely biomechanical, types of regulation which antecede a particular action by a minimal period of time, we apparently encounter extrapolation of the same type as that incorporated in a Taylor series with the use of two primary derivatives as information, that is, data from the joint and muscle signalling systems. (This is sometimes described as gradient extrapolation.) Considering more complex and meaningful types of plans for movements, such as may require reprogramming during their course, the higher co-ordinational brain systems and the synthetic processes involved will be found to include forms of probabilistic extrapolation among their equipment, and these will doubtless include just such methods of active sampling as have been formulated and described in the conactive sampling as have been formulated and described in the connon-local temporary mathematics of estimation as methods of non-local search [46]. It is necessary to emphasize the decisive difference in principle between the appearance in the physiology of activity, of extrapolational search which has been described above, and the concept of trial and error described by the behaviourists. The latter indicates a sequence of attempts, each of which is unrelated to preceding ones, and is, like them, made at random. In this case it is only the external form which is active, the sum of trials being essentially treated as a passive statistical computation of successes and failures. Figuratively, we may say that each trial of this sort gives information of the type "this is not the way", but gives no information as to where or how to do "what is necessary". It is no accident that this principle is easy to imitate in machine models. On the other hand active non-local search, which is apparently a real component of orientational behaviour, after the first couple of attempts are either made at random or else directed in some approximate way by elementary mechanisms working on the principle of gradient extrapolation, results in the deduction of how and where the next step must be taken. In this way each attempt renders more accurate a progress towards the optimum means by which the maximum amount of the most useful information can be obtained.

VIII

What is known at present in experimental physiology about the manifestations and effects of this model of the future, and by what experimental techniques may these best be described in the light of

exact modern knowledge? Let us turn again to the consideration of concrete examples of movements.

Among the multiplicity of functions of the central nervous system involved in the control of motor acts, the first to be explained are the processes by which movements are corrected while they are in progress. This is achieved by a system of feedback connections served by the numerous informational sources available to the body. The mediation of this uninterrupted system of correction is a most important biomechanical premise for the production of any purposeful motor act: the mastery of the enormous number of degrees of freedom possessed by our motor organs, and their conversion by these means into a directed system. This function may be regarded as the technical aspect of *motor co-ordination*.

During the course of the co-ordinational process (considered in micro-intervals both of time and of the path of the movement) one characteristic peculiarity of all excitable organs plays a decisive role. All such organs possess *finite* and also *variable* values of *thresholds of arousal*. The absolute values of these thresholds are remarkably varied for different organs, and for each particular organ they may further vary between wide limits, depending on overall physiological conditions.

This is a circumstance which has very important consequences for the control of motor acts. The central brain systems organizing and co-ordinating motor acts, primed by the wealth of information from sensory sources, are enabled to do more than correct such disagreements as may arise between intended and actual movements *post factum*. Proceeding with a determinate program of operation, the central nervous system can, and indeed does, achieve *anticipatory adaptations* in terms of the tuning in advance of the arousal of all the sensory and motor elements which are employed. These interesting but still barely investigated examples of regulation *ante factum* outstrip, as it were, movements by micro-intervals of time, and are closely bound up with the mechanisms of anticipation and extrapolation which have been discussed above. They have been described under various experimental conditions, and by various investigators, now as neuromuscular *tonus*, now as physiological *sets* and, in recent years, as functions of the reticular formation of the brain, although a growing amount of evidence suggests that we are here concerned with the same wide range of interrelated factors. In terms of contemporary electrophysiological techniques these pro-

cesses of anticipatory adaptation can only be observed with some difficulty and as disconnected manifestations. It is naturally most convenient to observe them *before the beginning* of a movement, when the weak bioelectrical manifestations of tonic commands are not masked by the far more powerful potentials accompanying muscular activity. These tonic impulses, which precede the beginning of a movement, are the neuromuscular concomitants of *sets*. Improvements in the techniques of recording bioelectrical phenomena in nerves and muscles will make it possible to study these processes of set (switching processes in Lapicque's metaphor) during the course of the entire motor act.

The most interesting problems in this area, which have only just begun to be considered, are naturally related to the central nervous regulation of processes which involve set. Some of the problems encountered in this area bring us once again, and in an unexpected way, to the central problem of the cerebral representation of reality, and of the types of coding which the brain imposes on its evidence. We approach this topic a little indirectly.

Physiologists have distinguished for some time between two very different forms of arousal process which exist concurrently in the neural and muscular substrate. One of these forms, which appears to be more recent in terms of evolutionary history (it may properly be called neokinetic), is manifested as a rhythmic sequence of bursts of excitatory impulses (sometimes called peaks, or spikes) following the all-or-none law. (That is to say, they have the same height, whatever may be the strength of the supraliminal stimulus impinging for the given variable degree of their excitability.) These impulses travel at considerable speeds (of the order of tens of meters per second), and are transmitted without damping along nerve fibres. Because these impulses are transmitted over the entire course of the reflex ring through fibres enclosed in isolating myelinated envelopes with dielectric properties, the neural impulse codes running along adjacent fibres in a nerve do not suffer from mutual interference or leakage. This allows us to regard them as a "*channelized*" form of nervous process.

A second manifestation of nervous activity in neurons and muscular units, which is much more ancient in terms of its appearance during phylogenesis (it may be called palaeokinetic) has retained, in man and the higher mammals, the monopoly of the control of the smooth musculature in internal organs, and has also taken over

the role of the tonic transmission of adaptational impulses to sense organs and effector apparatus, as discussed previously. These impulses differ sharply from neokinetic phenomena. Firstly, they are dosable, that is, they do not obey the all-or-none law; secondly, they have two types or signs of significance—or, in other words, they may promote either excitation or inhibition. Thirdly, their activity is not explosive—that is, instead of discrete peaks occurring at millisecond intervals they exhibit slow waves of various forms and heights. Finally, their most typical property lies in the fact that the dielectric coverings of the fibres *do not constitute obstacles* for their passage, so that they, or at least their major components, are able to spread *across the fibres*. For these reasons it is more correct to regard this form of nervous activity as being of *wave form* in distinction to the channelized form of neokinetic impulses. This latter property does not have much practical scope within the comparatively narrow peripheral nerve fibres. However, in the main brain mass itself we may say with some certainty that it is precisely these processes, penetrating considerable masses of brain tissue, and even the carapace of the skull, which are nowadays accessible to electroencephalographical investigation, being frequently called, in loose terms, *cortical bioelectrical currents.*

It is important to bear in mind that the neokinetic chains of impulses in the cortical neurons, being channelized and rigidly isolated from each other, cannot escape from their channels and appear on electroencephalograms (E.E.G. records). It is again unnecessary to make the point that encephalograms are quite unrelated, either in terms of their frequency or their overall form to chains of impulses of the all-or-none variety such as are observed in nerve fibres, and that they do not also represent the result of the superimposition of patterns of such activity upon each other. A whole range of clinical observations, particularly of cases of abnormal E.E.G.s accompanying pathological conditions, leaves little doubt that wave-form processes in the cortex play a certain important role in the regulation of channelized impulses. It is more than probable that this regulational activity is bound up with the function of the *reticular formation* of the brain, as we remarked earlier. We shall not consider this aspect of the problem any further—it is currently under extensive and successful investigation by experimentalists and clinicians. We may now choose another line of approach to the problem.

During the last 200 years the history of the science of brain function has undergone wide oscillations between two opposing points of view as to the relationship of these functions to the substrate of the brain. After the work of Flourens and his contemporaries in the first half of the 19th century, the final triumph of the anti-localizational point of view appeared to be assured—that is to say, there was a wide recognition of the wave type of brain processes, acting on an undifferentiated substrate. The discovery of the projection zones of the cortex (in about 1870) swung the pendulum sharply in the opposite direction. In particular, the accumulation of an ever-increasing amount of information about the primary projection areas led to the intensive development of all the theories of cellular centrism with which we have been earlier concerned in this chapter. The cortex began to be regarded as a highly differentiated receptacle solely for channelized processes taking place in neural conductors (axons) with corresponding cortical cells acting as trigger-buttons for actions in the motor sphere, and as storage receptacles for the acquisition of experience of the environment in the perceptual areas.

The narrowness of these concepts was so clear that even within the memory of the living generation of scientists, in the thirties of this century, the "extreme left" of antilocalization again raised its head (the schools of Lashley, Paul Weiss, *et al.*), attempting to demonstrate the concept of mass action of the cortical cells and to shift the centre of gravity of the study of nervous processes towards a search for specificity among the codes of impulses transmitted along the nerves in the brain mass itself.

There is now no reason to decide the question in terms of either of these extreme cases—to put the problem on an either/or basis. Although the enormous mass of data now available provides solid arguments in favour of both points of view, it would be useless to bring them to discussion, or to seek for reconciling solutions. It is time that the following was clearly understood.

The high degree of differentiation of the cortical substrate, particularly in the higher animals, is now beyond question. However, just because of this great conglomeration of active excitable neural elements packed in electrolytic substance, there exist all the necessary conditions for the development of wave processes acting trans-

versely to neural paths, and involving the interaction of very large numbers of these elements. It would further be difficult to deny that the greater the degree of morphological localizational differentiation and subdivision of the cortical substrate, the more favourable are the conditions for an intensive development upon it of non-localized wave processes. Any electrician who is concerned with alternating currents and fields will confirm that it is a real problem to protect, by means of shielding, the function of the aggregate apparatus from the effects of mutual inductance and capacitance between its components. This must naturally apply in a far greater degree to the extremely complex living ensemble within a fluid electrolytic mass, where properties and charges vary both as functions of time and of the co-ordinates of each of their points.

It would be incorrect to visualize wave processes in the cortex as macroscopic fronts which are comparable in extent with the size of the entire skull. On the contrary, in correspondence with the microscopic non-homogeneities of the brain mass, its variable electrical parameters, and the momentarily altering pattern of its potentials, one must regard these processes as having a very delicate lace-like spatial and temporal structure. Such fluctuations in potential which can be recorded through the skull as the E.E.G. are naturally no more than a fused "hubbub".

It is hard to doubt that the wave processes which are composed of innumerable transverse interactions between the neurons and conductive pathways of the brain are not dominated in some way by the tonic regulationary activity of the reticular formation, and possibly also of the cerebellum and of the cellular centres of the brain stem. In these areas there is certainly infinitely more to be learnt than has been investigated.

The whole of this discussion points to the necessity for the consideration by physiologists of the study of central-nervous processes as an indivisible synthesis of channelized and wave-form components, and this once again, and for the last time, brings us to the problem of models of brain action, and to the question of the separation of the observer and the percept.

Cellular centrists have always diligently avoided the problem as to what exactly may be said about the cells of secondary projection areas in respect to the content with which they are supposed to be entrusted. What (besides the indeterminate chronic excitation postulated by the conditioned reflex school) is imprinted upon a cell which

must store for months and years the images of chairs and lamps, and hypotenuses, or the terms for these things? If these contents are represented by the brain in the form of corresponding codes, then what determines the selection of an appropriate non-occupied storage cell for this code, and in what form is it retained?

The problem of the form taken by informational codes employed by the brain, and of their storage in the mechanisms composing memory, is still far from a solution. It is, however, necessary to approach it in terms of the most modern concept.

The falsity of the view of the opposition of the observer and the percept in the brain has already been emphasized. Instead of the passive expectation of information by an observer we now visualize active operators co-operating in synthetic and dynamic ways to capture information, and the modelling of preformulated and anticipatory actions. We now also expect to encounter, in place of stationary cells which select, and in some way store, microscopic atoms of a representation of the world, dynamically synthetic neural processes which are simultaneously multiply channelized and wave-like in form, and which we have hardly begun to consider in this way. There now appears to be more evidence for the view that the distinction between the cells of the brain (supposed initially to be empty and undifferentiated from each other), and the externally introduced and alien meaningful content, is just as inaccurate as the distinctions drawn between the internal observer and percept.

If every active process of perception and action is represented in the brain by the formation of a corresponding operator, then the most probable form which the latter may take is the formation of a determinate kind of contour, resulting in a new path for the circulation of both channelized and wave-form processes — a contour, the existence and characteristics of which are not determined by the nature of some hypothetical content of the cells, synapses, interstitial tissues, etc., but by the very dynamic form of its organization and connections. To put the matter as briefly and schematically as possible, we may say that the meaningful content and adequacy of a given portion of the model of the environment does not lie in what is or is not contained in it, but is no other than this operator, in the sense in which this term has been defined here.

The present account of the directions and problems confronting physiology does not pretend to fulfil the functions of a program, and so is not an exhaustive survey of the problems which exist in

this area. The problems of the *affective motivation* of voluntary actions and of the physiological relationship between affective activity and its conscious intellectual forms has also been entirely neglected. Further, it has also not been possible to include details of processes in which negative entropy is clearly expressed, such as in the development and growth of organisms, beginning at the stage of the impregnation of the ovum and the coding or modelling within it of the *future* organism which will grow out of it. We have neglected the cardinal problems of structuring, expressed in terms of the qualitative and quantitative interaction between schemas and (metrical) forms in the processes of growth and activity. Nevertheless if, within the range of problems on which this account touches, we may provoke ideas, crucial objections or counter-arguments which are important for future investigation, the purpose of this account will have been fulfilled.

TRENDS IN PHYSIOLOGY AND THEIR RELATION TO CYBERNETICS

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THE introduction and development of new methods in industry have acted as a spur to the new trends in physiology with which we are concerned in this article, and to the formulation of the general problems which led, after a series of attempts, to the establishment of cybernetics as a science. If, when we think of cybernetics, we have in mind not the doctrine of Wiener, Shannon, Ashby, etc., but a general science which is concerned with the regulation of complex systems in conjunction with information and communication (and it is this which we shall consider from now on), it will be seen that a considerable number of the problems confronting modern physiologists are closely related to the more general ones for which cybernetics was first intended.

As the amount of heavy physical labour steadily decreases in everydaywork applied biology, starting with the energetics of work, biomechanics, protection and hygienics of work, etc., has begun to turn its attention to problems concerning intellectualized work in man–machine complexes, rationalization of control and communication, distribution of function, etc., and it is precisely in elucidating such problems that the methods and concepts of cybernetics have turned out to be particularly valuable. An important area in modern applied psychophysiology is undoubtedly the study of work under conditions where very high demands are made on the subject's attention, adaptability and will, etc. (astronautics, high-speed flight, work at high altitudes, underwater or underground).

There are some recent offshoots of theoretical physiology which deserve mention and consideration here. The first one—the physiology of regulation—was established at about the same time as cybernetics and was to a certain extent its forerunner; the second

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